

INVESTIGATING ODONTOCETE OCCURRENCE AROUND OAHU AND MAUI NUI  
USING A MULTIMETHOD APPROACH

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## ABSTRACT

The distribution of odontocetes is largely driven by bottom-up ecological processes that in turn influence foraging opportunities. Environmental variables such as bathymetry may help indicate productive foraging regions, and thus serve as useful tools when assessing dolphin spatial and temporal patterns. To understand the effects of bathymetry and diel patterns on odontocete distributions in an understudied region of the Hawaiian archipelago, the Maui Nui (Maui, Lana‘i, Kaho‘olawe, Moloka‘i) and Oahu Islands, three methodologies were utilized: passive acoustic monitoring techniques, directed vessel-based surveys, and citizen science observations. Acoustic results showed that high-frequency whistling dolphins, verified by a signal classifier to represent smaller odontocetes, tended to occur closer to deep waters and followed strong diel patterns of activity. In contrast, more rare low-frequency whistling dolphins, confirmed to be larger odontocetes, were not influenced by diel patterns. They also typically distributed further from deep waters, except in the Maui Nui region, where no relationship with bathymetry was found. This lack of a trend was likely driven by interspecific habitat differences, as visual sightings showed that false killer whales (*Pseudorca crassidens*) were observed in shallow waters of approximately 100 m while short-finned pilot whales (*Globicephala macrorhynchus*) were found in deeper insular waters of approximately 650 m. Visual methods also indicated that, during the daytime, smaller species are typically found in shallow waters of 100 m to 300 m, which corroborates previous research on spinner dolphins (*Stenella longirostris*). When comparing the two visual approaches, depths of sightings were similar for the majority of species observed, reflecting the potential value of citizen science cetacean sighting projects. As a whole, this study provides insight into Hawaiian odontocetes’ use of

foraging and resting habitats relative to bathymetry around Maui Nui and Oahu, and demonstrates the value of a multi-method approach to reveal odontocete distributions.

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## PREFACE

Despite decades of cetacean research in the Hawaiian Islands, Hawaiian odontocetes, a diverse group of eighteen species, have largely been overlooked due to the difficulties of surveying such cryptic animals in frequently poor conditions. Field studies have been biased instead towards easily-visible and accessible cetaceans, including the charismatic humpback whale (*Megaptera novaeangliae*) during winter months and resting spinner dolphins (*Stenella longirostris*) during daytime hours. With little research funding available, field cetacean projects may become increasingly limited to those that either address a management issue and/or focus on easily accessible cetaceans that can guarantee results. Thus, it is critical to develop methodologies that make cetacean surveys more time- and cost-efficient. These alternative approaches will help shift the focus to better understanding the ecology of odontocetes, which occupy an important predator niche in the unique Hawaiian marine ecosystem.

The following chapters of this thesis present two novel approaches to study the spatial ecology of odontocetes around the Maui Nui (Maui, Lana‘i, Kaho‘olawe, Moloka‘i) and Oahu islands of the Hawaiian archipelago. Specifically, the distribution of odontocete species relative to bathymetry is addressed to provide further insight into possible dolphin foraging and resting habitat preferences. The first chapter describes the application of passive acoustic methods to determine spatial and temporal patterns of odontocetes at varying proximities to the 1000 m contour surrounding the region. In contrast with traditional visual survey observations, passive acoustic monitoring (PAM) allows for “acoustic” observations of dolphins, as sound is an accepted proxy of dolphin presence and propagates long distances through water. In addition, PAM projects are relatively unconstrained by environmental conditions and require little field effort, since autonomous recorders can be deployed and left for months at a time. While a major

shortcoming of previous PAM studies is their inability to provide taxonomic identification, this study provides a coarse resolution technique to acoustically distinguish large and smaller odontocetes and help determine the influence of bathymetry on their distributions.

The second chapter employs a “citizen science” approach to help understand odontocete interspecific depth preferences around the Maui Nui region. Recruiting volunteers to collect scientific data is becoming increasingly popular, yet it has been a relatively underutilized technique to help study cetaceans. This study enlists vessel operators, a typically untapped resource of marine knowledge, to report dolphin sightings. By comparing depths of community sightings to those made from systematic surveys of the region, citizen science can be validated as an alternative approach to traditional systematic dolphin surveys. In addition, the study contributes valuable insight into daytime odontocete habitat usage in the Maui Nui region.

**CHAPTER I**  
**PASSIVE ACOUSTIC METHODS**

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## **Abstract**

The distribution of odontocetes is largely driven by bottom-up processes that in turn influence foraging opportunities. Environmental variables such as bathymetry may help indicate productive foraging regions, and thus serve as useful tools when assessing dolphin spatial and temporal patterns. To understand the effects of bathymetry, season and diel variation on odontocete distributions, passive acoustic monitoring techniques were utilized near an understudied region of the Hawaiian archipelago, the Maui Nui (Maui, Lanaʻi, Kahoʻolawe, Molokaʻi) and Oahu Islands. Results showed that high frequency whistling dolphins, verified by a signal classifier as smaller species, tended to occur in proximity to deep waters and followed strong diel patterns. In contrast, rarer, low frequency whistling dolphins, confirmed to be larger species, typically distributed further from deep waters and were not influenced by diel trends. These acoustic findings support previous research showing that small dolphins such as *S. longirostris* track and forage upon the vertically migrating mesopelagic boundary layer community. They also likely use daytime rest areas in close proximity to deep waters. Conversely, insular populations of larger dolphins such as false killer whales may be able to forage more effectively in shallow waters further from slope regions. This work will help inform management decisions in Hawaii regarding critical odontocete habitat in light of growing concerns over dolphin tourism and fisheries operations.

**Keywords: Odontocete, Passive Acoustics, Spatial Ecology, Hawaiian Islands, Maui Nui, Bathymetry, Ecological Acoustic Recorder**

## Introduction

Odontocete distributions are driven by many factors, including breeding and calving opportunities, predation, and anthropogenic effects, but the strongest influence is the need to successfully forage (Acevedo-Gutierrez et al. 1997, Davis et al. 1998, Acevedo-Gutierrez & Parker 2000, Davis et al. 2002, Hastie et al. 2004, Richardson et al. 2013, Righi et al. 2013). The ability to forage effectively is in turn influenced primarily by bottom-up processes (Suryan et al. 2006, Azzellino et al. 2008). These may include direct effects from prey distributions (Heithaus & Dill 2002), such as the movement patterns of dolphins tracking the location of their prey (Acevedo-Gutierrez & Parker 2000), and may also include indirect influences by lower trophic levels including phytoplankton (Pardo et al. 2015), zooplankton and micronekton biomass (Davis et al. 2002), or from habitat features that may affect prey availability (Gowans & Whitehead 1995, Smith & Whitehead 1999, Brager et al. 2003, Pardo et al. 2015). Given the difficulties of collecting and analyzing data from wide-ranging oceanic prey (Acevedo-Gutierrez & Parker 2000, Heithaus & Dill 2002, 2006), studying the physiographic and hydrographic features that favor prey availability has become an effective means of examining the spatial patterns of occurrence of odontocetes (Torres et al. 2008, MacLeod et al. 2014, Copeland et al. 2016).

Many oceanographic features play a role in shaping odontocete distributions (Davis et al. 1998, Neumann 2001, Pardo et al. 2015) and bathymetric factors, in particular, have been shown to be effective proxies in capturing the spatial variation of cetaceans (Selzer & Payne 1988, Baumgartner 1997, Raum-Suryan & Harvey 1998), with water depth strongly tied to sightings (Davis et al. 1998). Steep slopes are generally linked with high occurrence rates of odontocetes (Ingram & Rogan 2002, Reid et al. 2003), as they may provide high concentrations of prey (Ballance 1992). However, the influence of water depth is more variable. Based on multispecies

assessments within an area, some odontocete species are tied to shallow waters while others occur more frequently in deeper waters (Mobley et al. 2000, Canadas et al. 2002). This interspecific variation likely results from different diets or foraging strategies, or competition for similar resources. There is some evidence that habitat partitioning between sympatric species may even occur on minute scales of only a few meters difference in preferred water depths (Parra 2006). Thus, considerable ambiguity may exist regarding the strength and direction of effect that bathymetry plays on the distribution of multiple odontocete species within a region.

The Hawaiian Islands offer a unique opportunity to study the influence of bathymetric variation on a diverse assemblage of sympatric odontocete species in a complex trophic system. The insular waters of the Hawaiian Islands experience increased productivity due to the “island mass effect,” the input of nutrients from freshwater runoff and wind curl upwelling (Doty & Oguri 1956). As a result of this productivity (Roger 1986), a distinct land-associated community of fish, shrimp, squid and other micronekton known as the mesopelagic boundary community layer (MBCL) surrounds the Islands where slope waters meet the oceanic environment (Reid et al. 1991, Benoit-Bird & Au 2003). This biomass-rich layer undergoes diel vertical and horizontal migration, with micronekton rising to the surface and towards shore at night and descending to depth during the day triggered by changing light levels (Forward & Barnes 1988, Benoit-Bird et al. 2001). A variety of predators utilize the MBCL for food, including both open-ocean and nearshore predators (Norris & Dohl 1980, Haight et al. 1993, He et al. 1997, Skillman et al. 1998). In addition to the MBCL, large pelagic fish are drawn towards the islands (Itano & Holland 2000), which support predators at the highest trophic levels.

In part due to the food resources provided by the mesopelagic layer, eighteen species of odontocetes occur in sympatric populations around the Hawaiian Islands (Table 1) (Mobley et al.

2000, Barlow 2006, Abecassis et al. 2015). These species can be loosely grouped into two cohorts by size and prey preferences. Smaller-bodied odontocetes, such as spinner dolphins (*Stenella longirostris*), are known to forage primarily on myctophid fish (Norris et al. 1994), which constitute a large portion of the MBCL. To best exploit the MBCL, spinner dolphin populations horizontally track the layer (Benoit-Bird & Au 2003), foraging during the night in depths of 200 to 250 m when the MBCL is closest to the surface and to shore (Fitch & Brownell 1968). They then return to shallow-water resting sites during the day (Norris & Dohl 1980, Norris et al. 1994). Most other smaller odontocetes also follow spatial and diel patterns that optimize resting and foraging opportunities, some similarly preferring shallow waters near productive slope waters. Other temporal factors may also interact with bathymetry to influence dolphin distributions. For example, numerous studies have documented seasonal shifts in habitat usage relative to water depth (Neumann 2001, Azzellino et al. 2008, Simard et al. 2015). Lunar phase may also affect dolphin distributions, as was shown by Benoit-Bird et al (2009), who found a positive relationship between the abundance of spinner dolphins and lunar illumination near the MBCL off Oahu.

Larger-bodied Hawaiian odontocetes are drawn towards the islands to exploit larger prey that also aggregate around the Hawaiian Islands as a result of the island mass effect (Shallenberger 1981, Connor & Norris 1982, Baird et al. 2008). These prey species include pelagic fish such as mahi mahi (*Coryphaena hippurus*), typically consumed by false killer whales (*Pseudorca crassidens*), as well as mesopelagic squid, commonly eaten by short-finned pilot whales (*Globicephala macrorhynchus*) (Pauly et al. 1998). Given the prey differences between small and large odontocetes as well as between *P. crassidens* and *G. macrorhynchus*, variation in preferred water depth may occur in nearshore Hawaiian waters among different



species. Indeed, visual surveys in insular waters have documented a shallow-water preference for false killer whales (Baird et al. 2008), perhaps reflecting increased foraging opportunities in shallow depths. Understanding how large odontocetes distribute in nearshore waters relative to bathymetry is important because insular false killer whales are known to compete for resources with trolling fisheries. Fisheries interactions have resulted in relatively high fin disfigurement rates for insular false killer whale populations, (Baird & Gorgone 2005, Baird et al. 2010), which have experienced steep declines in the past 20 years (Chivers et al. 2007, Baird et al. 2008). A clear understanding of the depth preferences of large odontocetes near heavily utilized Hawaiian coastlines could help guide proper management of these small, vulnerable populations.

Although a few studies have directly addressed the relationship between bathymetry and odontocete occurrence in Hawaiian waters (e.g. Baird et al. 2013, Abecassis et al. 2015), past studies have relied solely on visual observations. Because cetacean visual surveys in Hawaiian waters are affected by frequently poor surface conditions due to prevailing trade winds, the accessibility of certain areas in the archipelago is often restricted. In addition, some cetacean species occur in small groups or surface infrequently, making them even more difficult to detect in rough seas (Buckland et al. 1993, Baird et al. 2013). As such, results of visual surveys around the Hawaiian Islands may be subject to some inherent bias.

Passive acoustic monitoring techniques hold potential as an alternative approach to overcome some of the limitations in visual surveys. Since many marine mammals are extremely vocal, acoustic signals are generally considered a good proxy for documenting the presence of delphinids in the tropics (Rankin et al. 2008, Richardson et al. 2013). Sound can also propagate long distances through the ocean (Medwin & Clay 1998), potentially allowing recorders to detect odontocetes across a several kilometer-wide area. In addition, the frequency of dolphin whistles

is related to species body size, so whistles can be used to identify both small and larger bodied odontocete species (Azzolin et al. 2014). Finally, given that autonomous acoustic recorders can be fixed and can record for long durations, their use allows for a more synoptic and long-term examination of how odontocetes utilize an area over space and time (Hodge et al. 2013, Simard et al. 2015).

This study utilizes a passive acoustic monitoring approach to assess the relationship between bathymetry and the spatiotemporal occurrence of odontocetes within the Oahu and the Maui Nui (Maui, Lana‘i, Kaho‘olawe and Moloka‘i) regions of the Hawaiian Islands. These five islands are encircled by the 1000 m isobath and are characterized by comparatively shallow interior waters that drop off sharply at the 1000 m isobath (Figure 1). Given the heterogeneity in habitat created by this drop-off, the effect of bathymetry was assessed according to the proximity to deep waters, with autonomous acoustic recorders placed at varying distances to the 1000 m isobath. Recorder depths were relatively similar; thus, proximity of the recorders to the 1000 m isobath was used as a more appropriate bathymetric factor to study the horizontal movements of odontocetes relative to this isobath over time.

The dolphin populations occurring off Oahu and Maui Nui have historically been the least studied of around the Hawaiian Islands. This is in large part due to their low diversity, with only ten and eight species, respectively, of the eighteen species that occur in Hawaii typically documented in these two areas (Baird et al. 2013). However, both large- and small-bodied species do occur in the region, and thus the distributions of both cohorts can be investigated with respect to bathymetry. Spatially, the acoustic data help address the question of whether differences occur in the insular distributions of small and large odontocetes relative to the 1000

m isobath. Temporally, the data help reflect whether the spatial dynamics of these odontocete cohorts also follow seasonal and/or diel patterns.

## **Methods**

### Acoustic Deployments

Passive acoustic monitoring was carried out around Oahu and Maui Nui using Ecological Acoustic Recorders (EARs), which are bottom-moored, autonomous devices programmed to record on a duty cycle (Lammers et al. 2008). For this project, all EARs were set on a 10% duty cycle, with 30-second recordings made every five minutes. EARs were either programmed at a sampling frequency of 125 kHz or 64 kHz. Both bandwidths are sufficiently broad to capture the whistle fundamental frequencies of all Hawaiian odontocetes and the lower frequency components of echolocation clicks (Oswald et al. 2004). EARs were deployed at four sites off the coast of Oahu between 2009 and 2011 and at eight sites around the Maui Nui region between 2015 and 2016 (Figure 1). Sites were chosen to represent a gradient of nearest distances to the 1000 m isobath. Around Maui Nui, acoustical coverage of the ‘Au‘Au, Pailolo and Kalohi channels was also considered to examine the role these channels play in the movement patterns of odontocete species.

Each Oahu EAR deployment spanned a period of three to four months, and four deployments were made at each site. Around Maui Nui, EARs were deployed during different seasons for one to three months. However, the EARs at sites MauiNui4 and MauiNui6 malfunctioned and each recorded for only six and twelve days, respectively. The MauiNui6 EAR was deployed a second time in the same location, while the MauiNui4 EAR site was moved 8 km to the east to more effectively cover the Kalohi Channel, thus becoming become site MauiNui8.

## Data Processing

After each deployment, EAR recordings (referred to as files) were downloaded and analyzed visually as spectrograms using the Matlab-based program, *Triton* (Wiggins 2007). A trained analyst scanned spectrograms for the presence of dolphin clicks and/or whistles using a 10-second display window and the widest possible bandwidth. If signals were detected, the file was given a call abundance score based on the number of whistles and/or the duration of dolphin echolocation clicks within the file (Table 3). Files with whistles were also classified as either low frequency (LF; all energy < 10 kHz), high frequency (HF; all energy > 10 kHz) or high frequency and low frequency (HFLF), a transitional ambiguous category with whistle energy both above and below 10 kHz. Low frequency whistles are indicative of the presence of larger bodied species, while high frequency whistles are indicative of the presence of one or more smaller species of odontocetes (Table 1) (Azzolin et al. 2014). Files designated “HFLF” may either indicate the presence of both large and smaller bodied species or a single species producing whistles of frequencies across the 10 kHz threshold.

The three files with the highest call scores, representing the highest rate of signaling, were then selected for each hour of dolphin activity. Based on the three files with the highest scores, the hour was classified as containing clicks, HF, LF or HFLF whistles, or some combination of whistles and clicks. When an hour contained both low and high frequency whistle files or ambiguous whistles, the hour was classified as ambiguous.

## Data Analysis

### *The Effects of Proximity to the 1000 m Isobath and Seasonality on Oahu Dolphin Whistle Occurrence*

To assess bathymetry as a predictor of different dolphin whistle types, it was first necessary to analyze the effects of other spatial and temporal co-varying factors on whistle occurrence. In contrast to the Maui Nui data, the extensive temporal coverage of the Oahu EARs made these data more appropriate to use for this analysis. It is assumed that the variables influencing the Oahu data had a similar relationship with the Maui Nui data, given the proximity of the islands.

LF and HF daily whistle hours were each averaged by month and then modeled separately using mixed linear models with site and year as random effects. Clicks and HFLF whistles were disregarded for this analysis since their taxonomic classification was ambiguous. Averaging daily whistle hours by month helped to remove the majority of the autocorrelation between consecutive days of recording without compromising variation in whistle occurrence on a longer time scale. Average daily hours of each whistle class were log-transformed and their distributions were found to be approximately normal. Season and proximity to the 1000 m isobath were chosen as predictor variables in each initial mixed linear model. Lunar illumination was initially to be included in the model as well, yet averaging the whistle data on a monthly scale made it unfeasible to assess possible effects of daily changes in lunar cycle. Each month was categorized to either Fall (September through November), Winter (December through February), Spring (March through May) or Summer (June through August). Site and year were also included in the model as random effects. EAR site distance to the 1000 m isobath, accounting for intervening landmasses, was determined using the function “dist2isobath” within

the R programming package “marmap” (Table 2). The three predictors were plotted and examined visually using the “effects” package. Using the “r.squaredGLMM” function in the “MuMIn” package, the marginal and conditional variances explained by the predictors and overall models were then generated and compared.

#### *The Effects of Proximity to the 1000 m Isobath on Whistle Occurrence*

The ability to predict variation in whistle occurrence relative to bathymetry was explored and compared by whistle type and island region, with distance to the 1000 m isobath as the sole predictor variable. Similar to the previous analyses, mixed linear models were again utilized, and four were constructed for HF Oahu, LF Oahu, HF Maui Nui and LF Maui Nui. The models were plotted and examined visually, and the significance of distance to the 1000 m isobath as a predictor variable was determined using a Type II Wald chi square test with the function “Anova” in the “car” package.

#### *The Effects of Diel Variation on Whistle Occurrence*

To examine overall diel trends in the occurrence of different whistle types, HF and LF whistle presence hours were pooled across EAR sites by island region. Histograms were created and visually assessed for the total hour counts of each whistle type binned by each hour of the day (0000-2300). To account for proximity to the 1000 m isobath in diel variation, Maui Nui and Oahu EAR sites were binned into one of the following groups based on their location: “Near” (0-15 km from the 1000 m isobath), “Moderate” (16-31 km), and “Far” (32+ km). The count of HF and LF whistle hours from each group by hour of the day were again visually examined using histograms. To examine the statistical relationship between the count of night versus day dolphin

detections, only three hours in middle of the night (2300-0159) were compared with three hours in the middle of the day (1100-1359). This was to ensure that the potential transition periods of dawn and dusk did not confound the diel analysis. The observed whistle detections for both the night and day periods were compared to expected detections by whistle type, proximity category and island region using a two-tailed G-Test using Yates' continuity correction.

#### *Real-Time Odontocete Call Classification Algorithm (ROCCA) Analysis*

To validate the assumption that low frequency whistles were indicative of the presence of larger species and that high frequency whistles were indicative of smaller species, whistles were classified using the Real-Time Odontocete Call Classification Algorithm (ROCCA) (Oswald et al. 2007). ROCCA is used to extract contours of delphinid whistles and measures their features, which function as inputs for a random forest based classifier used to identify each whistle to a species (Oswald & Oswald 2013). Whistle classifications are then grouped by a user-defined “encounter” of dolphins, and the overall species encounter classification is determined based on the summed results of all whistle classifications within that encounter.

Two EAR deployments from Maui Nui with low ambient noise levels and a high rate of whistle detections per encounter were selected to subsample using ROCCA. For this analysis, an encounter was defined as an hour of the day during which dolphins were present and whistling. Encounters were excluded from the analysis if fewer than 20 whistles were present within the encounter. In addition, if fewer than 20 whistles were present between gaps of 30 or more minutes within the encounter, the encounter was also excluded. If more than 40 whistles occurred within an encounter, whistle files were randomly chosen for analysis until the 40-whistle threshold was crossed. Due to the particular interest in endangered insular false killer

whales, all low frequency whistle encounters in these two data sets were analyzed using ROCCA. Ten high frequency and four ambiguous encounters were also randomly selected for classification.

## Results

In total, 536,832 files were recorded on the four Oahu EARs. Considered hourly, 10,960 hours of recordings (24.7%) contained either dolphin echolocation clicks or whistles, and therefore were classified as positive dolphin hours (PDH). From the Maui Nui region, 77,760 files were recorded from six of the eight sites. Data from EAR site MauiNui4 were excluded from statistical analyses, as a data set of six days was considered too small to properly represent dolphin occurrence at that site. In addition, MauiNui1 data was only processed for whistle detections, as the strong acoustic presence of snapping shrimp across the high frequency spectrum contributed to masking of dolphin echolocation signals. Of the recorded Maui Nui files, 8,208 hours (28.7%) contained dolphin signals. Therefore, the frequency of signal occurrence was regularly similar between the two island regions.

When positive dolphin hours were examined by call type across all sites (Figure 2), the mean proportion of HF hours (mean=0.475, sd=0.109) constituted the majority of PDH, while the mean proportion of LF hours (mean=0.102, sd= 0.075) accounted for a much smaller fraction. The mean proportion of click hours (mean=0.417, sd=0.106) was similar to that of HF whistles, and thus it can assumed that those clicks were predominately produced by high frequency whistling dolphins. Of all call types, HFLF ambiguous hours made up the smallest proportion (mean=0.065, sd=0.049). The trends did not change when Oahu data were examined independently of Maui Nui data.



*The Effects of Proximity to the 1000 m Isobath and Seasonality on Oahu Dolphin Whistle Occurrence*

The following HF mixed linear model was constructed and plotted by predictor for the Oahu data set (Figure 3).

$\text{lme}(\text{formula} = \text{Hfavg} \sim \text{Season} + \text{DistanceTo1000} + (1|\text{Site}) + (1|\text{Year}, \text{family} = \text{gaussian})$

In the model, “Hf avg” is a continuous variable indicating the daily count of HF whistle hours averaged on a monthly scale, “Season” is a categorical variable of the season of the recordings, “DistanceTo1000” is a continuous variable of the proximity of the EAR site to the 1000 m isobath, “Site” is a random categorical factor for each EAR site, and “Year” is a random categorical factor for the year of the recordings. Based on the plots, there is a clear negative trend between HF monthly hourly means and distance to the 1000 m isobath (Figure3a). Some seasonal variation exists as well (Figure3b), with slightly lower HF means during the Spring and Winter.

The marginal and conditional variances from the overall model explained the most variation in the HF whistle data ( $R^2_m=0.258$ ,  $R^2_c=0.427$ ). When assessed by predictor, a Type II Wald chi square test showed that “DistanceTo1000” was the only significant predictor of HF means ( $\chi^2=4.35$ ,  $p<0.05$ ). When the models were reconstructed with each individual predictor versus HF mean, season explained high conditional variation in the data but low marginal variation ( $R^2_c=0.443$ ,  $R^2_m=0.053$ ). In contrast, DistanceTo1000 explained a relatively high degree of both marginal and conditional variation in the data ( $R^2_m=0.215$ ,  $R^2_c=0.393$ ).

Based on these results, the temporal factor of season was considered to have relatively little effect on HF means compared to proximity to deep waters.

To assess variation in LF mean whistle hours, a similar mixed model was created with the same predictors and “Lfavg,” the daily count of LF whistle hours averaged on a monthly scale, as the response variable:

```
lme(formula = Lfavg ~ Season + DistanceTo1000 + (1|Site) + (1|Year), family = gaussian)
```

Based on plots of these predictors, little variation existed between seasons (Figure4b) with the exception of summer, which appeared to correspond with higher LF means. However, a strong positive relationship was apparent between distance to deep waters and LF whistle hours (Figure4a).

The overall model again had the highest marginal and conditional variances ( $R^2_m=0.233$ ,  $R^2_c=0.233$ ), yet the random effects had no influence on the variation in the data. Based on individual contributions of each predictor, DistanceTo1000 again was the only significant factor in the estimate of the effects of the predictors on LF mean ( $\chi^2=17.518$ ,  $p<0.001$ ). In addition, models of each predictor showed that both the marginal and conditional variation explained by proximity to depth ( $R^2_m=0.207$ ,  $R^2_c=0.207$ ) were nearly the same as those of the model as a whole. Thus, similar to the HF data, LF whistle hours clearly varied more spatially relative to bathymetry than temporally relative to season.

### *The Effects of Proximity to the 1000 m Isobath on Whistle Occurrence*

Given the findings of the previous analyses, it was concluded that proximity to the 1000 m isobath was likely the primary predictor of HF and LF whistle hour occurrence, and that it was reasonable to model the effects of only this predictor on whistle occurrence in both the Oahu and Maui Nui data sets. Similar to prior analyses, four mixed linear models were constructed by island region (Oahu, Maui Nui) and by whistle type (HF, LF). Based on plots of HF means versus distance to the 1000 m isobath (Figure 5), there was a clear negative relationship between proximity to deep water and HF occurrence for each region. Type II Wald chi square tests confirmed that the estimate of the negative effect of proximity to deep water was significant for Oahu (effect estimate=-0.036, chi sq=4.599,  $p<0.05$ ) and for Maui Nui (effect estimate=-0.040, chi sq=4.072,  $p<0.05$ ). Thus, distance to deep waters is a suitable proxy for predicting the occurrence of HF whistles within the Oahu and Maui Nui regions, with greater occurrence of HF whistle hours at EAR sites closer to deep waters.

When mean LF whistle hours were modeled and plotted relative to proximity to deep waters for Oahu and Maui Nui (Figure 6), there was a clear positive relationship for Oahu (effect estimate=0.011, chi sq=17.518,  $p<0.001$ ) but little pattern for Maui Nui (effect estimate=0.0037, chi sq= 0.207,  $p>0.05$ ). Given the small sample size of the data in the model ( $n=18$ ) coupled with sparse daily LF whistle hours, the lack of significance for Maui Nui is not surprising. Based on the more robust Oahu results, it can be concluded that proximity to deep waters does correlate with LF whistle occurrence, but that this relationship is positive, as opposed to the negative trend seen with HF whistle occurrence. Obtaining a larger sample size of LF whistles would help determine whether the same trend also exists in the Maui Nui region.

### *Effects of Diel Variation on Whistle Occurrence*

Diel analysis of HF detections pooled by island region revealed strong differences in nighttime versus daytime detections, with fewer detections made during the day. At Maui Nui sites (Figure 7a), gradual changes in detection count occurred during the dawn and dusk transition hours, with minimum detections at hour 1300. In contrast, there was an abrupt reduction in detections from night to day at Oahu sites (Figure 7b), which gradually increased again in the late afternoon. For LF detections, there was no clear diel pattern at the Maui Nui sites, with substantial variability during both daytime and nighttime hours (Figure 8a). LF detection counts from Oahu sites showed a slight diel trend (Figure 8b), with a peak in acoustic encounters around dusk.

When HF diel trends at Maui Nui EAR sites were further examined based on proximity to the 1000 m isobath, patterns observed at the “Near” (Figure 9a) and “Mid” (Figure 9b) sites were generally similar to those for the pooled HF detections. However, the trend became less apparent for sites “Far” from the 1000 m isobath (Figure 9c), with little apparent difference in detection counts between night and day hours. For each island region, there were significantly more nighttime detections for the “Near” and “Mid” categories than day detections (Table 4). However, for the “Far” category, there was no significant difference between the count of daytime and nighttime encounters, which supports the apparent lack of a diel trend observed in the “Far” histogram.

The counts of nighttime and daytime LF whistle detections (averaged hourly) were also not significantly different from each other for any of the distance categories with the exception of the Maui Nui “Mid” bin, which had significantly more night than day detections. The lack of significance for the majority of the distance categories further corroborates the variable diel

pattern of detections observed in each LF histogram. Overall diel temporal variation occurs in HF whistles, but its effects vary spatially. For LF whistles, it appears that diel variation is not an important variable influencing whistle occurrence.

### *Real-Time Odontocete Call Classification Algorithm (ROCCA) Analysis*

Based on ROCCA analyses of encounters from MauiNui2 and MauiNui5, those manually and visually classified as “LF” (n=30) resulted in a definitive species classification of false killer whale (*P. crassidens*) for all encounters except for one from MauiNui2, which was classified as short-finned pilot whale (*G. macrorhynchus*). Thus, encounters containing whistles with the majority of their energy below 10 kHz indicate the presence of these two larger species. For the “HF” encounters (n=20), nine were classified as spinner dolphin (*S. longirostris*), 10 as bottlenose dolphin (*Tursiops truncatus*) and one as pantropical spotted dolphins (*S. attenuata*). All encounters containing whistles of a frequency mostly above 10 kHz were thus classified as these three smaller-bodied odontocetes. Finally, not surprisingly, analysis of the ambiguous “HFLF” encounters produced species classifications of both large and smaller odontocetes. Of the eight HFLF encounters analyzed, four were classified as *P. crassidens* and four were categorized as *T. truncatus*. The equal classification of small and large odontocete species for HFLF whistles reaffirms the transition and somewhat ambiguous nature of this whistle category.

### **Discussion**

Based on the evidence presented, it does appear that the spatial ecology of odontocetes off Oahu and in the Maui Nui region is linked to the bathymetry of the islands. This relationship varies by species, as proximity to deep waters on Oahu was found to influence smaller-bodied

HF whistling dolphins inversely from its influence on false killer whales, the predominate species classification of LF whistles. In Maui Nui, however, no association was documented between proximity to deep waters and LF dolphin presence. In addition, the two signaling cohorts exhibited different diel patterns, with HF whistling dolphins showing strong diel trends, particularly when close to deep waters. However, these trends broke down further inshore from the 1000 m isobath. In contrast, LF whistling dolphins showed little diel pattern, regardless of location. These findings indicate that small dolphins tend to distribute towards the 1000 m isobath, especially during nighttime foraging hours, while large dolphins either distribute more haphazardly or closer towards shore in shallower waters.

Given that the two signaling cohorts differ in prey preference (e.g. Shallenberger 1981, Benoit-Bird 2004), the results also suggest differences in prey distributions and/or prey capture strategies among dolphin species. Based on ROCCA analyses, HF dolphin whistles were classified as *T. truncatus* and *Stenella* species, and these species were identified more commonly on EARs close to deep water. Along the steep slopes of the Hawaiian Islands, the 1000 m contour is closely associated with the MBCL, which, during the day, occurs over bottom depths of 400 to 700 m and extends horizontally many kilometers (Reid et al. 1991, Benoit-Bird & Au 2003). Small dolphins such as *S. longirostris* feed extensively on this dense prey layer as it rises to shallower depths and moves towards shore at night, and need to consume several small prey items per minute to meet their energy needs (Benoit-Bird 2004). During the daytime, spinner dolphins show strong daytime affiliations to specific coastal areas, particularly with respect to the 100 m contour (Lammers 2004, Thorne et al. 2012). Thus, to meet their energetic quota, these species likely move from nearshore resting areas towards the 1000 m isobath in the evening hours in order to intercept the MBCL and maximize foraging time. Based on this study

as well as previous work, it can be inferred that spinner dolphins may prefer daytime habitats that are close to offshore feeding grounds to minimize transit between resting and foraging habitat (Norris & Dohl 1980, Thorne et al. 2012). Although spinner dolphins have been studied extensively around Hawaii Island (e.g. Norris et al. 1994) and Oahu (Lammers 2004), this is the first study to document the habitat preference of spinner dolphins in waters around Maui Nui. This study also suggests that areas away from the deep isobath may offer limited prey resources for small delphinids and therefore represent less desirable foraging habitat, although the extent of the nocturnal horizontal migration of the MBCL into shallow waters is still poorly understood and warrants further investigation.

Although some odontocetes may shift their distributions seasonally (e.g. Azzellino et al. 2008, Simard et al. 2015), seasonality had little influence on the acoustic distribution of small species in the Maui Nui and Oahu regions. This agrees with prior assessments of Hawaiian odontocetes that also failed to document any strong seasonal trends in distributions (Baird et al. 2013). While lunar phase changes could have affected odontocete spatial patterns, averaging hourly daily detections by month made it unfeasible to examine the potential effects of this temporal factor. Given that Benoit-Bird et al. (2009) documented increasing spinner dolphin abundances in Hawaii around the MBCL with increasing lunar illumination, it would be interesting to investigate the interaction of lunar phase with bathymetry with a different passive acoustic monitoring (PAM) design. The only temporal factor examined that influenced the distribution of small odontocetes was the time of day, with HF whistle detections being more common during the nighttime hours compared to the daytime hours. The diel variation in HF whistle occurrence coincides with the diel migration of micronekton in the MBCL, as small odontocetes synchronize their foraging to the rise of organisms in the evening (Norris & Dohl

1980, Benoit-Bird 2004). This diel trend was strong at EAR sites closest to the 1000 m isobaths, and therefore closest to the MBCL, but more variable by hour at sites greater than 30 km away from the 1000 m contour. It can thus be inferred that smaller odontocetes are likely only transiting through and/or only foraging opportunistically in waters furthest from the slope region. However, their presence at night so far away from deep waters is interesting and suggests that some components of the MBCL may migrate horizontally quite far inshore.

In contrast with HF whistling species, the strength of the effect of bathymetry on LF whistling odontocete presence is more ambiguous, given that results differed between Maui Nui and Oahu EAR sites. All LF dolphins were classified by ROCCA as large odontocetes, with *P. crassidens* representing the majority of detections. In the Oahu region, proximity to the 1000 m isobath had a strong positive relationship with the presence of this acoustic cohort, with greatest occurrence rates furthest from the isobath. Large delphinids around Oahu thus followed an inverse trend from that observed for smaller dolphins. These results corroborate visual surveys of *P. crassidens* in insular waters, with more sightings in depths of 0 to 500 m than 500 to 1000 m (Baird et al. 2013), which further supports that the LF dolphins recorded around Oahu were primarily false killer whales. Given the considerably smaller number of LF encounters compared with HF encounters, our results also indicate that large species are much less common than smaller species in shallow water regions. It may be inferred, then, that large odontocetes typically inhabit offshore pelagic waters, which previous studies also support (Baird et al. 2008). However, the productivity created by the “island mass effect” of the Hawaiian Islands (Reid et al. 1991) enhances foraging opportunities, thus occasionally drawing large-bodied dolphin species towards coastal waters. Within these nearshore waters, mahi mahi, the primary prey of false killer whales, forage upon epipelagic nekton and aggregate near floating objects and



artificial fish aggregating devices (FADs) (Wickham et al. 1973, Olson & Galvan-Magana 2002), suggesting that they have a haphazard distribution. Given our acoustic findings on Oahu showing increased LF dolphin occurrence further from the 1000 m isobath, two scenarios are possible. First, mahi mahi may actually concentrate closer to shore within insular waters, increasing foraging opportunities for *P. crassidens*. Alternatively, individuals of the insular population of *P. crassidens* may utilize shallow waters strategically to capture mahi mahi more effectively. This is the first study to posit such a theory for false killer whale feeding behavior, and more research is needed to investigate this idea in greater depth.

Around the Maui Nui Islands, variation in LF dolphin occurrence was not significantly related to distance to the 1000 m isobath, suggesting that the acoustically-detected larger delphinids may have been composed of both false killer whales and short-finned pilot whales. Whereas this study suggests that false killer whales may forage most effectively along shallow contours, short-finned pilot whales are known to perform deep dives in pursuit of cephalopods, which in turn forage upon the MBCL (Pauly et al. 1998, Aguilar Soto et al. 2008, Abecassis et al. 2015). Insular *G. macrorhynchus* are thus intrinsically linked with waters along the 1000 m isobath to effectively forage upon dense prey patches (Abecassis et al. 2015). A study examining visual sightings from citizen scientists and also systematic surveys provides further support for differing habitat preferences among the larger delphinids, with false killer whales typically being seen in waters approximately 100 m deep and short-finned pilot whales being observed in waters greater than 600 m (Howe et al. in prep). Therefore, niche partitioning by these two larger odontocete species likely contributes to the lack of a bathymetric trend in the Maui Nui region. Another possibility to explain the lack of a relationship is that LF whistling dolphins around Maui Nui do follow a similar pattern to those around Oahu, but that our LF whistle sample size

was not large enough to capture the trend. While the Maui Nui acoustic data sets contained robust spatial coverage, each data set recorded for a relatively short time frame compared to the Oahu deployments. Given that LF signals were uncommon overall, variation in the Maui Nui region relative to proximity to deep waters may not have been captured in this data set. Regardless of the effects of distance to the 1000 m isobath, little diel variation existed in the occurrence of LF whistling dolphins in both regions. This further illustrates the dietary differences between the two dolphin cohorts, with large species pursuing epipelagic nekton likely during both daytime and nighttime hours and smaller species preying at night upon micronekton undergoing daily vertical migration.

This study also demonstrates the value of PAM techniques to reveal trends in odontocete distributions. To date, only a few spatial ecology studies have implemented PAM methods and these have successfully documented both seasonal and daily dolphin movements relative to depth and also corroborated the patterns with visual sightings (Simard et al. 2015, Hodge et al. 2013). While visual surveys are typically limited in their temporal coverage and can only document dolphins during daytime hours, our PAM methods allowed for both day and nighttime observation of our study area. In addition, the extended recording abilities of these devices allowed us to capture both short and long term temporal trends in odontocete occurrence and relate these to broader ecological patterns. On the other hand, acoustic data likely underestimates dolphin occurrence, as recorders will not capture the presence of silent animals (Hodge et al. 2013). It would be useful to investigate vocalization rates of large versus small odontocete species to assess how the presence of silent animals may have influenced the results of this study. In addition, acoustically sampling dolphin presence with a duty cycle can negatively impact the accuracy of call rate estimates and acoustic presence, especially for sparsely occurring

calls (Thomisch et al. 2015). As a result, LF calls may have gone undetected and underestimated in this study. Despite these potential biases, acoustic methods offer an alternative approach to examine dolphin distributions, and may provide the most comprehensive results when used in conjunction with visual surveys (Norris et al. 2006).

In the past, a major limitation of PAM techniques was that recorded signals were unidentifiable to species due to high inter-species signal variability. Passive acoustic recordings made in areas with multiple sympatric species thus contained only information about the presence or absence of dolphins generally. However, the development of the whistle-based classifier ROCCA by Oswald et al. (2007) has helped provide additional species information regarding these signals. In particular, ROCCA classifies bottlenose dolphins and false killer whales with a high degree of confidence, and these constituted the majority of our HF and LF encounters, respectively. In addition, the classification uncertainty of encounters in this study with both high and low frequency whistles reflects the importance of recognizing ambiguous encounters when visually scanning through spectrograms. When encounters of larger species need to be distinguished from those of smaller species for future passive acoustic studies, such ambiguous encounters should be excluded from analyses.

These results can also help guide management of anthropogenic activities around odontocetes in nearshore Hawaiian waters. In particular, dolphin tourism is a thriving industry, as companies are able to capitalize on the strong affiliations of resting spinner dolphins to specific areas (Lammers 2004, Hu et al. 2009). Consequently, direct human dolphin encounters are increasing in Hawaii, which may result in distress or avoidance behaviors in the animals, potentially leading to an energetic cost (Bejder et al. 2006, Courbis & Timmel 2009, Thorne et al. 2012). As spinner dolphins tend to choose resting habitat in proximity to their foraging

grounds (Thorne et al. 2012), the findings of this study suggest that certain areas around Maui Nui and Oahu, such as La Perouse Bay and Makua Beach, both well-known hotspots of spinner dolphin sightings, serve as critical habitat for the dolphins. Given the relative lack of prior odontocete research in the Maui Nui region, this work provides only an initial contribution to our understanding of small odontocete distributions in the region; more research is needed to specifically address questions of preferred spinner dolphin habitat around Maui Nui.

In addition, both small and large Hawaiian odontocetes face potential interactions with fisheries, especially in the Maui Nui region, which experiences one of the greatest recreational and charter fishing pressures of all the islands (Baird et al. 2013). Large tunas commonly associate with pantropical spotted dolphin groups, and thus fisherman use spotted dolphins as cues for productive fishing areas (National Research Council 1992). Due to the large number of vessels observed daily fishing around spotted dolphin groups and numerous dolphin hookings, Baird (Baird 2016) has suggested that local fisheries may be harming spotted dolphins. While more information is needed on these encounters, the present study provides a framework to better understand the distribution of spotted dolphins around insular Oahu and Maui Nui, which in the future could help with managing dolphin-fisheries interactions. For the endangered insular population of false killer whales, fisheries interactions are thought to occur primarily with trolling boats from nearshore operations, as little overlap has been found with longline fisheries and the MHI population (Baird et al. 2015). These encounters have produced scarring on 7.1% of the Moloka‘i *P. crassidens* cluster and 12.8% of the Lana‘i cluster (Baird et al. 2015). Based on the trends presented in this study around Oahu and other efforts in the Maui Nui region (Howe et al. in prep), *P. crassidens* are likely utilizing shallow, nearshore habitat to feed on large pelagic fish. Given the overlap in fish targeted by both recreational fishermen and false killer whales,

this insight into *P. crassidens* foraging behavior helps to explain the detrimental encounters documented with fishing operations.

The results of this study have implications for utilizing PAM techniques to understand other marine systems as well. Foraging is generally considered the strongest driver of odontocete distributions (Hastie et al. 2004). Thus, documenting the occurrence of dolphin species according to body size using acoustic methods provides valuable insight into their behavioral ecology as well as the ecology of their prey. In the Hawaiian Islands, acoustic monitoring combined with prior knowledge of prey preferences and their distributions provides evidence for habitat partitioning and variable foraging strategies by odontocetes relative to bathymetry and time of day. While interspecific differences in habitat preference have been shown previously using sighting data (e.g. Davis et al. 2002, Parra 2006, Azzellino et al. 2008), few studies have used acoustic odontocete detections to assess the influence of habitat features on spatial and temporal patterns. Around other island archipelagos with comparable physiographic features, fish resources and micronekton layers along slope regions, odontocetes could be expected to distribute in similar patterns as those presented in this study. Relatively low-cost, PAM approaches could be used to explore these habitats and would be particularly useful for developing nations and in understudied coastal regions around the world.

## **Acknowledgements**

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Finally, we would like to thank the Hawaii Institute of Marine Biology for lending us equipment to aid with our acoustic recorder deployments.

## Tables and Figures

*Table 1. Odontocete species documented in the Hawaiian Islands during surveys made by Barlow 2006 and Baird et al. 2013. Size classification based on approximate differences between species.*

Common Name	Scientific Name	Size Cohort	Present in Maui	Present in Oahu
<i>Stenella attenuata</i> (offshore)	Pantropical Spotted Dolphin	Small	x	x
<i>Stenella coeruleoalba</i>	Striped Dolphin	Small		
<i>Stenella longirostris</i>	Spinner Dolphin	Small	x	x
<i>Steno bredanensis</i>	Rough-toothed Dolphin	Small	x	x
<i>Tursiops truncatus</i>	Bottlenose Dolphin	Small	x	x
<i>Grampus griseus</i>	Risso's Dolphin	Small		
<i>Lagenodelphis hosei</i>	Fraser's Dolphin	Small		
<i>Peponocephala electra</i>	Melon-headed Whale	Large	x	x
<i>Feresa attenuata</i>	Pygmy Killer Whale	Large		x
<i>Pseudorca crassidens</i>	False Killer Whale	Large	x	x
<i>Globicephala macrorhynchus</i>	Short-finned Pilot Whale	Large	x	x
<i>Orcinus orca</i>	Killer Whale	Large		
<i>Physeter macrocephalus</i>	Sperm Whale	Large		
<i>Kogia breviceps</i>	Pygmy Sperm Whale	Large		
<i>Kogia simus</i>	Dwarf Sperm Whale	Large	x	x
<i>Mesoplodon denirostris</i>	Blainville's Beaked Whale	Large		x
<i>Ziphius cavirostris</i>	Cuvier's Beaked Whale	Large		
<i>Indopacetus pacificus</i>	Longman's Beaked Whale	Large		

Table 2. Summary of EAR parameters for Oahu and Maui Nui deployments.

Site	Number of Deployments	Distance to 1000m Isobath (km)	EAR Version	Sampling Frequency (kHz)	Sampling Duration (sec)	Sampling Period (sec)	Total Recording Duration (Hrs)
MauiNui1	1	43.4	2	125	30	360	1752
MauiNui2	1	14.3	2	125	30	360	816
MauiNui3	1	28	2	125	30	360	792
MauiNui4	1	24	2	125	30	360	144
MauiNui5	1	9.28	2	125	30	360	720
MauiNui6	2	30.4	2,1	125,64	30	360	1344
MauiNui7	1	40.7	1	64	30	360	1392
MauiNui8	1	30.8	1	64	30	360	1392
Oahu1	4	4.3	1	64	30	360	11112
Oahu2	4	3.8	1	64	30	360	9672
Oahu3	4	7	1	64	30	360	12720
Oahu4	4	24.7	1	64	30	360	10920

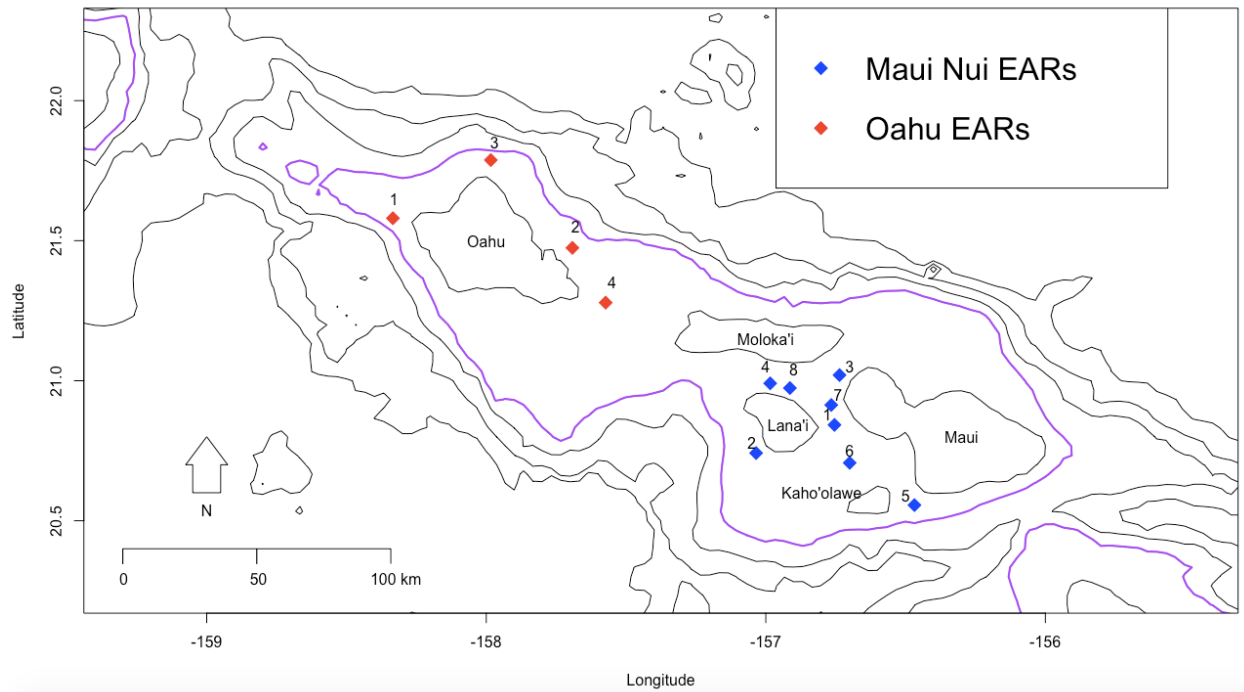
*Table 3. Call abundance scores assigned for 30 second recordings.*

<b>Category</b>	<b>Call abundance score</b>
1-5 whistles	1
Burst pulse (BP) only <5	1
Sonar only <1/2 recording	1
6-10 whistles	1.5
Sonar only >1/2 recording	1.5
BP only >5	1.5
Sonar & BP <5	1.5
1-5 whistles & sonar or BP	2
>10 whistles	2.5
Sonar & BP >5	2.5
1-5 whistles, sonar & BP	3
6-10 whistles & sonar or BP	3
6-10 whistles, sonar & BP	3.5
>10 whistles & sonar or BP	3.5
>10 whistles, sonar & BP	4

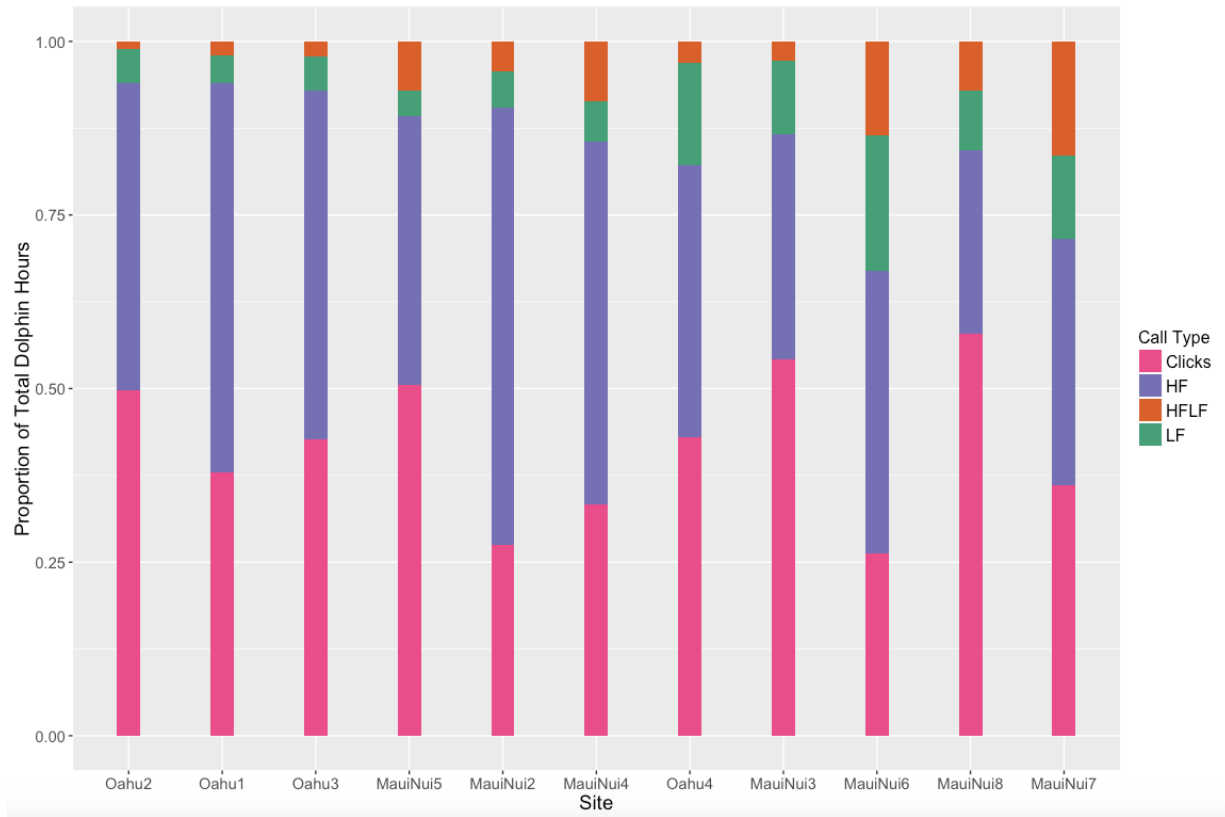


*Table 4. Summary of G-Test results for count of HF detections during the night (2300-0159) and day (1100-1359) by EAR site depth category and island region. Significant results are indicated with a \*.*

Whistle Type	Island Region	Depth Category	Night	Day	G Score	P-value (two-tailed)
HF	Oahu	Near	743	267	232.455	<<<0.05*
		Mid	108	43	28.003	<<<0.05*
		Far	NA	NA	NA	NA
	Maui-Nui	Near	92	17	55.059	<<<0.05*
		Mid	93	10	74.947	<<<0.05*
		Far	31	18	2.969	0.085
LF	Oahu	Near	56	52	0.083	0.773
		Mid	36	42	0.321	0.571
		Far	NA	NA	NA	NA
	Maui-Nui	Near	9	6	0.267	0.303
		Mid	22	6	8.472	0.0036*
		Far	14	7	1.783	0.187

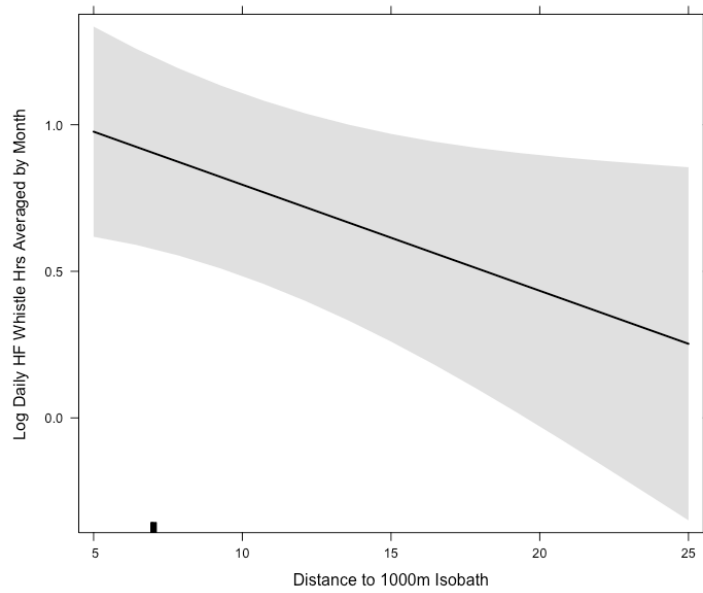


*Figure 1. Oahu and Maui Nui EAR sites. Oahu EARS were deployed between 2009 and 2011, while Maui Nui EARS were deployed between 2015 and 2016. The first 1000 m isobath is denoted in purple, and subsequent 1000 m isobaths are denoted in black.*

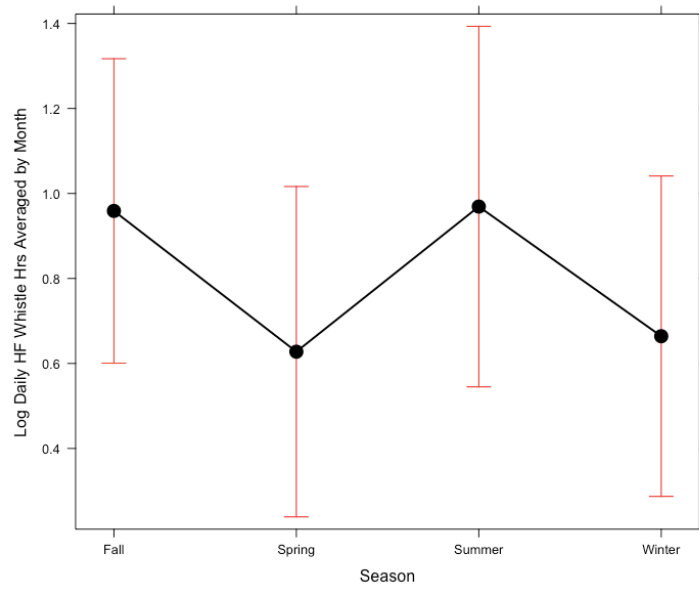


*Figure 2. Summary of Oahu and Maui Nui EAR recordings by call type and site. Sites arranged in increasing distance from 1000 m isobath.*

(a)

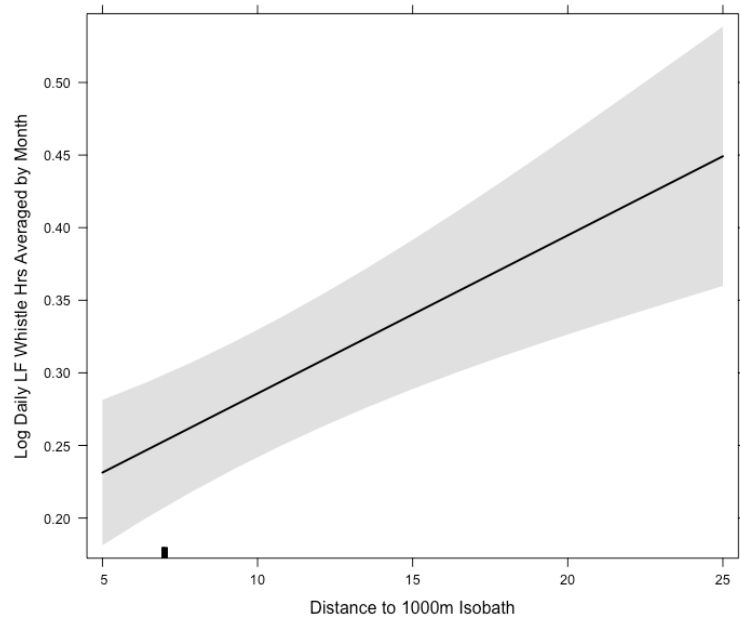


(b)

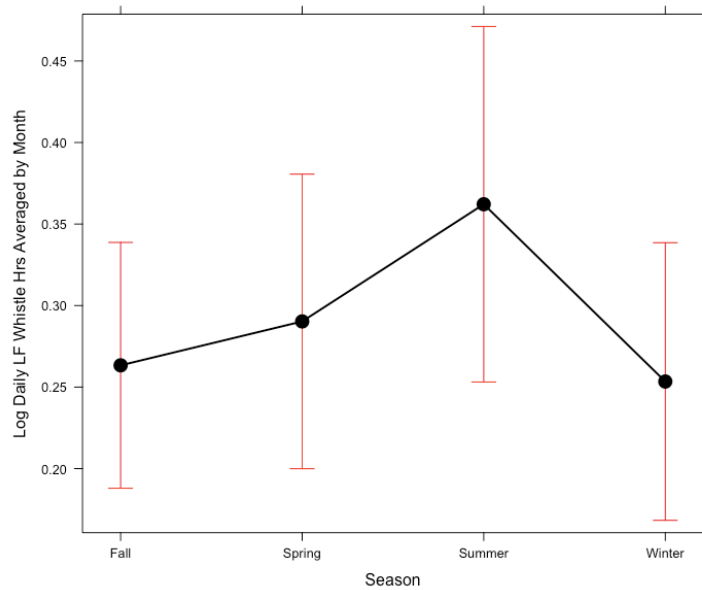


*Figure 3. Plots of effects of Distance to 1000 m Isobath (a) and Season (b) on Oahu log daily HF whistles hours averaged by month. Distance to 1000 m is the only significant predictor of HF whistles.*

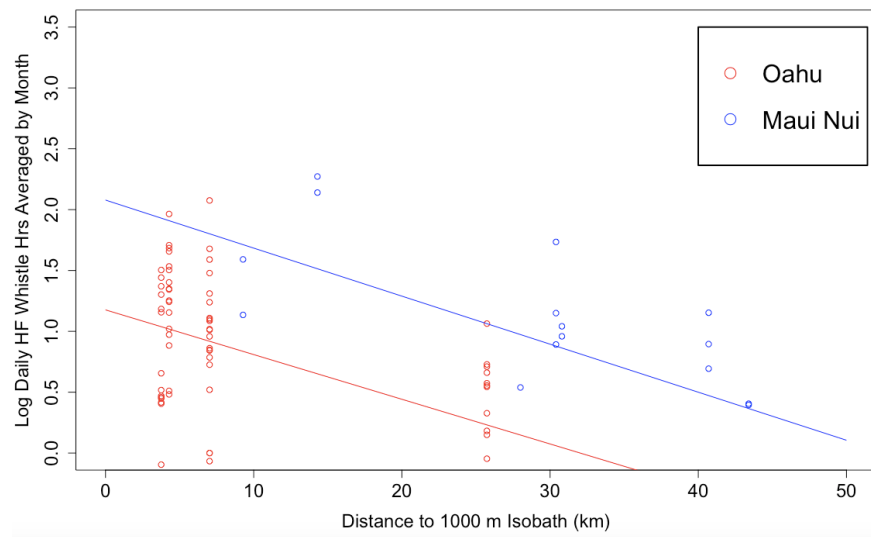
(a)

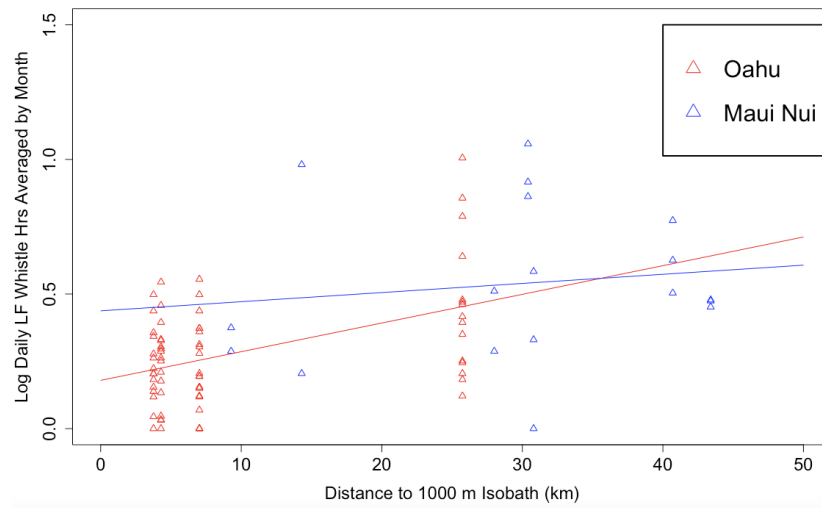


(b)



*Figure 4. Plots of effects of Distance to 1000 m Isobath (a) and Season (b) on Oahu log daily LF whistles hours averaged by month. Distance to 1000 m is the only significant predictor of LF whistles.*





*Figure 6. Linear regression models of Maui and Oahu LF whistle hours vs distance to depth plotted with observed values of log daily LF whistle hours averaged by month. Proximity is a significant positive predictor of LF whistle hours in Oahu but this relationship is not significant in Maui Nui.*

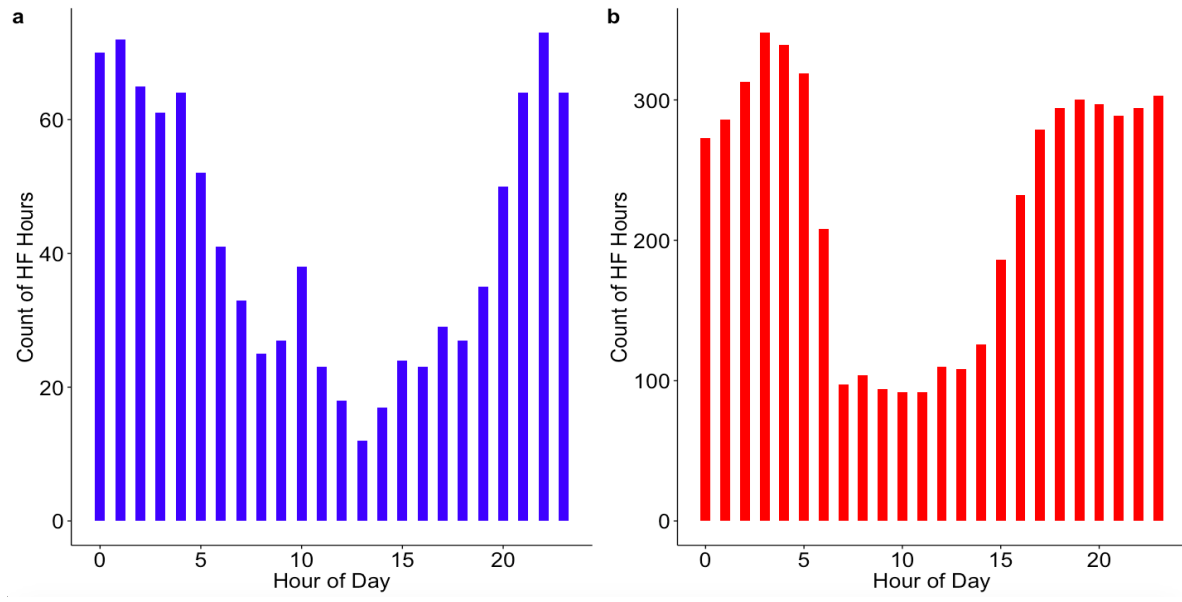
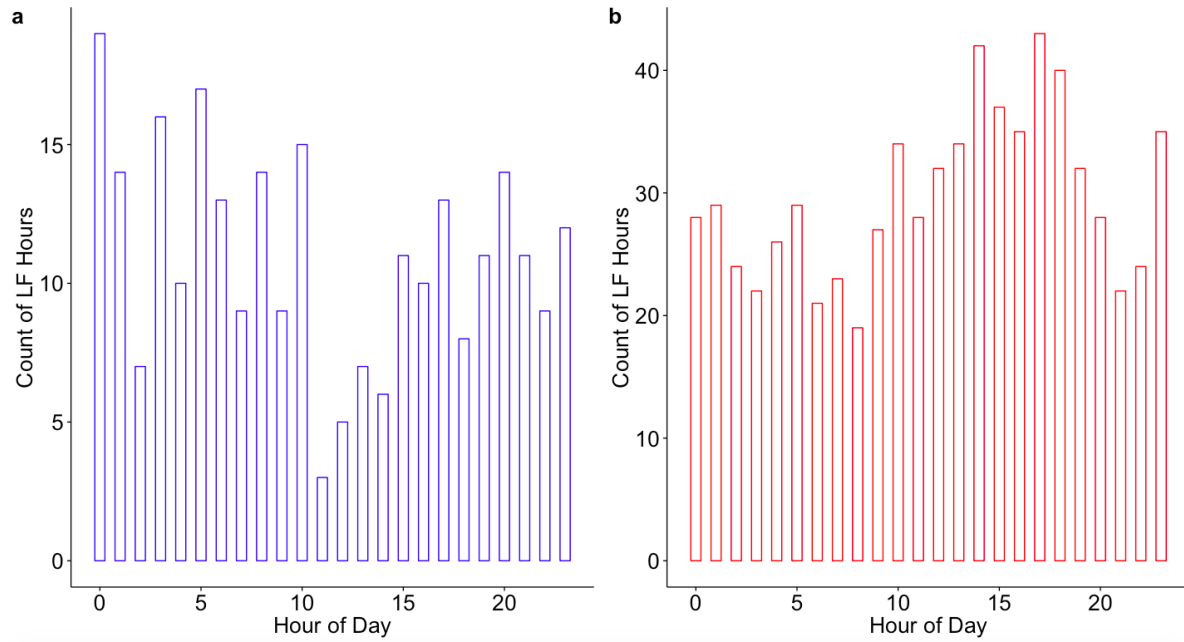


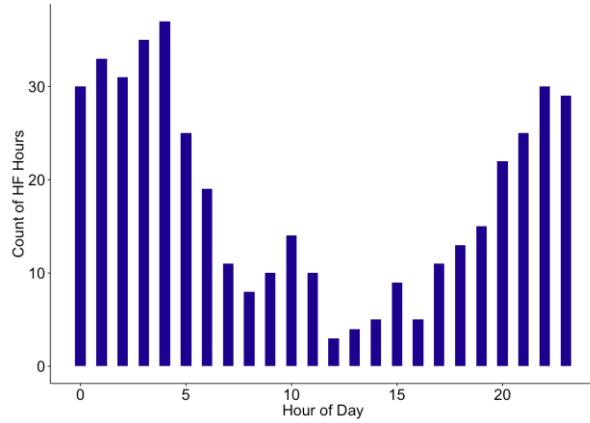
Figure 7. Total count of HF hourly encounters pooled across EAR sites in Maui Nui (a) and Oahu (b) by hour of day.



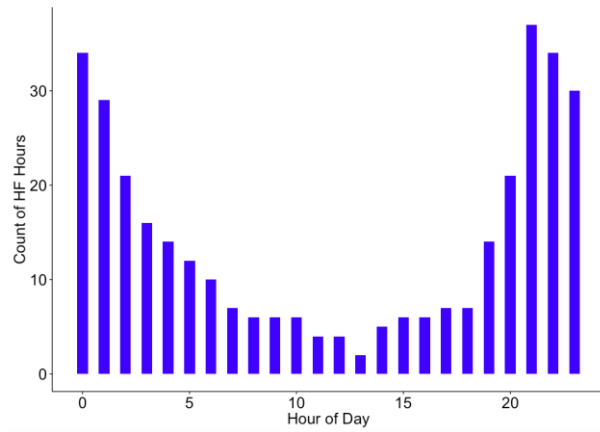


*Figure 8. Total count of LF hourly encounters pooled across EAR sites in Maui Nui (a) and Oahu (b) by hour of day.*

(a)



(b)



(c)

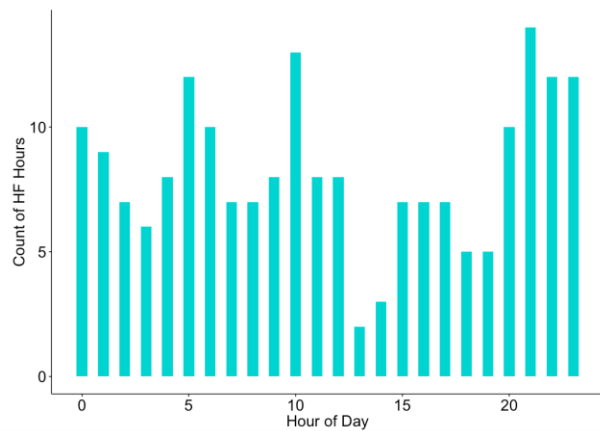


Figure 9. Count of HF hourly encounters in Maui Nui by hour of day at “Near” EAR sites 0 to 15 km from 1000 m isobath (a), “Mid” sites 16 to 31 km from isobath (b) and “Far” sites greater than 32 km from isobath (c).

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## **CHAPTER II**

### **CITIZEN SCIENCE AND DIRECTED SURVEY METHODS**

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## Abstract

Given the difficulties and costs often associated with surveying cetaceans, enlisting “citizen scientists” to collect data offers a promising alternative approach with proper project design and implementation. Furthermore, validation of cetacean citizen science with traditional scientific studies contributes to the robustness of the results. The Hawaiian Islands offer an ideal study site to employ such a dual-method approach to better understand the distribution of Hawaiian odontocete species relative to bathymetry. This study capitalized on the abundance of vessels operating in the shallow, understudied Maui Nui region (Maui, Lana‘i, Moloka‘i, Kaho‘olawe) by recruiting crew members and captains to report sightings of dolphins via text messaging. In addition, dolphin sightings were made by biologists during directed surveys in the same region. Depths of sightings were determined post-hoc and compared between methods for the most common species. Observations from the two methods had similar depth ranges for all species except spinner dolphins (*Stenella longirostris*) and short-finned pilot whales (*Globicephala macrorhynchus*), which was likely the result of differences in the distribution of vessel effort between the two methods. However, both methods indicate that pilot whales occur in the deepest areas around the Maui Nui region, pantropical spotted dolphins (*Stenella attenuata*) are found at intermediate water depths, while bottlenose dolphins (*Tursiops truncatus*), false killer whales (*Pseudorca crassidens*) and spinner dolphins occupy areas of shallower depths. The results of this study demonstrate the potential value of citizen science and of using a multimethod approach to reveal dolphin distribution trends relative to bathymetry in areas where both methods are feasible.

**Keywords: Odontocete, Citizen Science, Bathymetry, Maui Nui, Spatial Ecology, Visual Surveys**

## Introduction

“Citizen science” (CS) is a burgeoning field that utilizes volunteers to collect scientific information and help answer questions that otherwise would be logistically or financially unfeasible (Bhattacharjee 2005, Dickinson et al. 2010). In return, the public becomes more aware of conservation issues and gains a sense of “earth stewardship” (Dickinson et al. 2012). As charismatic megafauna, cetaceans are the focus of many citizen science projects. These include shore-based monitoring studies to determine habitat use and temporal variation (Evans & Hammond 2004, Pierpoint et al. 2009), stranding surveys to document mortality events and stomach contents (Gannon et al. 1997, Ford et al. 1998, Mignucci-Giannoni et al. 1999, Mignucci-Giannoni et al. 2000, MacLeod et al. 2005), and social surveys of fishermen to understand cetacean interactions with fisheries (Baird et al. 2002, Negri et al. 2012). Due to their ongoing popularity, some CS marine mammal programs have been occurring for decades, such as SeaWatch in the UK and the Great Whale Count in Hawaii. Given the costs and inherent difficulties of studying cryptic marine animals, tapping into a large-scale workforce of volunteers has resulted in greater spatiotemporal coverage of cetacean data, which in turn have led to numerous peer-reviewed articles (e.g. Gannon et al. 1997, Ford et al. 1998, Baird et al. 2002, Cheney et al. 2013).

CS cetacean studies are prone to numerous biases, however, and thus results must be critically evaluated when drawing inferences. Taxonomic identification of species is typically required of marine mammal studies, but this can have questionable accuracy, as cryptic, unusual, or similar species can often be confused (Bell 2007, Kelling 2008). Non-random distributions of volunteer effort and under-detection of species may also skew data (Crall et al. 2011). While studies comparing data generated by volunteers versus experts typically show comparable

estimates (e.g. Delaney et al. 2008), only one cetacean study has compared frequency of dolphin sightings made by volunteers to those made during systematic surveys (Bristow et al. 2001). In addition, only about half of published CS studies include some sort of verification process to ensure data quality (Thiel et al. 2014). To address the issue of data quality, some cetacean studies have compared and combined several independent citizen science approaches, allowing for estimation of biases by method and providing more robust scientific conclusions (Baird et al. 2002, Cheney et al. 2013), yet more multimethod assessments are needed.

Numerous opportunities exist to enhance the capabilities of CS cetacean projects to produce more comprehensive and robust scientific data. Captains and crew of commercial vessels offer a valuable resource to marine mammal studies, as they are generally familiar with their local waters and marine fauna and thus may more accurately identify species. In addition, data such as sighting coordinates collected by volunteers on vessels may be analyzed post-hoc relative to other biological data such as water depth to better understand cetacean habitat preference. Finally, advances in mobile technology have helped streamline marine field efforts, with Short Message Service (SMS) “text messages” now used to relay information from tagged animals as well as to report catch and effort information from fishermen (McConnell et al. 2004, Cronin & McConnell 2008, Baker & Oeschger 2009). Text messaging thus holds great potential in CS projects as an easy, cost-efficient, real-time communication tool to help facilitate data reporting (Baker & Oeschger 2009).

Around the Hawaiian Islands, much of the cetacean science by both citizens and experts has centered on the charismatic humpback whale (*Megaptera novaeangliae*), while odontocetes have received comparatively less attention due to their cryptic natures and low densities (Baird et al. 2013). While several single species studies have been conducted by biologists around the

Islands, largely focused on spinner dolphins (*Stenella longirostris*) (e.g. Norris et al. 1994, Benoit-Bird & Au 2003, Lammers 2004, Thorne et al. 2012), relatively few comprehensive, systematic multispecies assessments have been made of the eighteen dolphin species known to inhabit Hawaiian waters (Barlow 2006). The only published small vessel survey data of the Hawaiian odontocete community in coastal waters comes from the Cascadia Research Collective (Baird et al. 2013), who have spent a decade surveying the insular Hawaiian region documenting and studying odontocete species. Their results showed inter-species differences in the depth ranges of dolphins, with most species sighted more frequently in deeper slope waters greater than 1500 m. However, relatively little effort has been made in the shelf of the Maui Nui region (Maui, Lanaʻi, Molokaʻi, Kahoʻolawe), an area of high commercial tour boat and fishing vessel traffic. Thus, this area remains understudied with much still to be described and learned about how odontocetes use this distinct, Hawaiian shallow water environment. Because bathymetry is an important criterion of habitat selection by dolphins, enhancing foraging success or providing protection from predators (Davis et al. 1998, Davis et al. 2002, Hastie et al. 2004, Thorne et al. 2012), understanding the interspecific distribution of dolphins in this region of substantial human activity can help guide odontocete management.

This study implemented a citizen science dolphin-sighting project in the Maui Nui region, capitalizing on the numerous vessel crew and captains operating in the region to report dolphin sightings around the four islands. In addition, existing dolphin observations collected via dedicated surveys by the Cascadia Research Collective around Maui Nui allowed for a comparative analysis of the two methods, thus corroborating the CS project and providing a more robust understanding of dolphin distributions in insular Hawaiian waters.

## Methods

At the beginning of June 2015, the captains and/or crew members of sport fishing and commercial tour vessel operators were approached at the launch ramps and harbors along the leeward coast of Maui, including Kihei Boat Ramp, Mā‘alaea Harbor, Lahaina Harbor, Mala Boat Ramp, and Kā‘anapali Beach Entry. The purpose of the community sighting project and the ecological importance of odontocetes were explained and discussed with the crew. If a captain or crewmember expressed interest in participating in the project, he/she was given a laminated protocol sheet that reiterated the project goals and procedures. The protocol asked for several key pieces of information whenever a dolphin group was sighted in the Maui Nui region, including: 1) the date, the time of day and the GPS coordinates of the vessel; and 2) an identification of the species using a dorsal fin photo key of the most common species in the area, which included spinner dolphins (*S. longirostris*), bottlenose dolphins (*Tursiops truncatus*), pantropical spotted dolphins (*S. attenuata*), false killer whales (*Pseudorca crassidens*) and short-finned pilot whales (*Globicephala macrorhynchus*). It was requested that all sighting information be communicated via SMS text messages. If an observer was uncertain about the identity of the species, they were encouraged to send photos of the dolphins along with the data. The project lasted for six months through November 2015. Updates and reminders were periodically communicated to all observers involved in the project.

In addition, a database of sightings was used that was compiled during directed odontocete surveys conducted in the leeward Maui Nui region by the Cascadia Research Collective during one to six week periods in 2000, 2001, 2002, 2003 and 2012 (for full survey procedures see Baird et al. 2013). Survey areas were chosen to maximize geographic scope and depth range within the basin of the four islands, as well as to maintain relatively calm conditions

with minimal swell (<3 Beaufort). While on survey effort, two to six observers scanned 360 degrees around the vessel primarily with the naked eye and occasionally with binoculars. When an odontocete group was spotted, GPS coordinates and time of day were recorded, and the group was approached for identification. In addition, photographs were taken of the encounter, particularly when a group was difficult to identify to species level.

All sightings from both survey approaches were compiled and filtered. Species that were observed only once using either method were discarded from the analysis. In addition, sightings were excluded if they were made outside of the 1000 m isobath, the designated edge of the Maui Nui region in this study. Possible duplication of sightings from the community project was minimized by discarding all sightings reported for the same species occurring within a 5 km radius during the same hour on the same day as another sighting. With the corrected sighting information, water depths were generated for each encounter using the GPS coordinates input in the “get.depth” function from the R package “marmap.” Depths of sightings were compared by method across all observed odontocete species using an unpaired two-sample test. The specific test, either a parametric Student’s t-test or a non-parametric Wilcoxon sum rank test, was determined on the basis of the normality of the data visually assessed via histograms. Data were then pooled across methods and median depths of sightings were examined relative to species.

## **Results**

Observers participating in the community dolphin project reported 320 total sightings of six species including bottlenose dolphins, spinner dolphins, pantropical spotted dolphins, false killer whales, short-finned pilot whales and melon-headed whales (*Peponocephala electra*). Sightings were made between 0600 and 1800. Only one sighting was made of *P. electra* so the

species was removed entirely from the depth analysis. Thirty-seven observers representing 24 different vessels participated in the project. The vessels included 19 commercial tour operators and 5 sport-fishing operations. Half of the sightings came from just three observers, while the average number of sightings for the other 34 observers was considerably lower (mean=4.3 +/- 3.7). When observations were corrected for duplicate sightings, the total number of sightings decreased to 276 independent reports. Figure 1 shows the location of these sightings plotted in the Maui Nui region by species. The most frequently sighted species were spinner dolphins (n=151) followed by bottlenose dolphins (n=83) and pantropical spotted dolphins (n=30), while short-finned pilot whales (n=5) and false killer whales (n=7) were the least often sighted (Figure 3). July had the greatest number of observations (n=97), with reporting effort diminishing each subsequent month until the end of the project.

Five Maui Nui survey periods conducted by the Cascadia Research Collective resulted in 111 total sightings of eight odontocete species including, in addition to the those observed by the community observers, rough-toothed dolphin (*Steno bredanensis*), and dwarf sperm whale (*Kogia sima*). As with the community project, sightings were only made during daytime hours. Only one sighting was made each of *P. electra*, *S. bredanensis* and *K. sima*, so these three species were excluded from further analysis relative to depth. Figure 2 shows the location of the remaining 108 sightings plotted in the Maui Nui region by species. Across all surveys, the most commonly observed species was the bottlenose dolphin (n=60), while false killer whales (n=4) and spinner dolphins (n=9) were the least sighted (Figure 3), in contrast with the large number of spinner dolphin reports from the CS project.

When depths were resolved for all dolphin encounters, the distributions of data points were skewed for most species, and thus the non-parametric Wilcoxon rank sum test was chosen

to compare sighting depths between the systematic survey approach and the community sighting project for each species. Test results showed that the two approaches produced significantly different sighting depths of spinner dolphins ( $W=1104.5$ ,  $p<0.05^*$ ) and short-finned pilot whales ( $W=77$ ,  $p<0.05^*$ ), with directed surveys sighting pilot whales and spinner dolphins in deeper waters than community observers (Figure 4). However, for the other three species, there were no significant depth differences between the two survey types ( $W_{\text{bottlenose}}=2824.5$   $p=0.1715$ ,  $W_{\text{spotted}}=351$   $p=0.0862$ ,  $W_{\text{falsekiller}}=9.5$   $p=0.4487$ ). Median depth values of sightings by method relative to species are shown in Table 1. When data were pooled across both methods and examined by species, pilot whales were typically seen in the deepest waters (Figure 4), while pantropical spotted dolphins were found at a more moderate depth. The other three species (bottlenose dolphins, spinner dolphins, and false killer whales) were all observed in relatively similar, shallower waters of approximately 80 m. Median depth values of sightings by species combined across methods are shown in Table 1.

## **Discussion**

The Maui Nui dolphin community sighting project was successful in generating a large data set of dolphin sightings from five different species and fostering interest in the lesser-known cetaceans of Hawaii. The request for minimal sighting information combined with the ease of text message reporting likely contributed to the large number of observations made by many vessel operators. Reporting was initially high during the beginning of the project and peaked a month after its start date, but sightings did steadily decrease over the course of the project. Rather than a reflection of the actual abundance trends of dolphins in Maui Nui, this decrease is likely a reflection of diminished reporting over time, with crew likely occupied by other



responsibilities and forgetting to report. Sharing unusual sightings with all volunteers or creating reporting incentives, such as prizes for the most sightings, may have helped maintain reporting levels throughout the project. The few observers that submitted the majority of the reports may have also initially been more interested in marine science and/or dolphins, or perhaps were compelled by greater personal satisfaction (Thiel et al. 2014).

When the depths of community sightings were compared with those from directed odontocete surveys there was no difference for the majority of species, including pantropical spotted dolphins, false killer whales, and bottlenose dolphins. This suggests a general soundness of the CS approach and an overall robustness of the results to reveal trends in dolphin distributions relative to bathymetry. However, spinner dolphins and short-finned pilot whales were both sighted in significantly deeper waters during directed surveys than by the community sighting effort, which may be due to different distributions of effort. For example, to find spinner dolphins for their passengers, tour operators often transit across relatively shallow depths, since spinner dolphins are known to occupy shallow coastal areas during the daytime (Norris et al. 1994, Lammers 2004, Thorne et al. 2012). In contrast, the Cascadia Research Collective surveys in the Maui Nui region targeted less common odontocete species and thus took place further away from the coastline. This accounts for the relatively small sample size of spinner dolphin observations from these surveys. For pilot whales, different distributions of effort likely led to the considerable difference in total sightings, with CS vessels typically not transiting near the majority of the Cascadia Research Collective's pilot whale sightings along the shelf regions of Maui Nui. Indeed, all CS pilot whale observations were opportunistically made by fishing vessels, which engage in more offshore transits than tour operators. A larger sample size of CS pilot whale sightings, including more observations from fishing vessels, may have produced

results more similar to the scientific surveys. Non-random distributions of effort are a common issue with CS projects (Crall et al. 2011), and this bias was clearly apparent in both the community sighting approach and the Cascadia Research Collective directed surveys. The results suggest that a comprehensive survey would need to randomly distribute effort over both deep and shallow waters of the archipelago.

Other than the well-studied spinner dolphin, which requires protected, shallow areas during daylight hours to rest (Norris et al. 1994), little is known about the preferred depth range of the odontocete assemblages near the Hawaiian Islands. This is due to the resources and effort required to visually survey such cryptic marine animals in areas with consistently strong winds and poor sighting conditions. Although passive acoustic monitoring in insular waters around Hawaii has recently revealed distribution differences relative to bathymetry between larger-bodied odontocetes and smaller species (Howe & Lammers in prep), the results of this study contribute useful scientific information regarding the daytime distribution of additional odontocetes around Maui Nui, further elucidating the acoustic findings. Based on this study, pilot whales appear to occupy primarily offshore areas, likely in order to forage more efficiently on their epipelagic squid prey (Pauly et al. 1998, Abecassis et al. 2015). In contrast, false killer whales tend to prefer the shallower depths in the region, perhaps as a foraging strategy to capture their prey, which consists of larger fish such as mahi mahi (*Coryphaena hippurus*) and tuna (*Thunnus sp.*) (Shallenberger 1981, Connor & Norris 1982, Baird et al. 2008). Interestingly, based on both nearshore and offshore surveys, the Cascadia Research Collective typically sighted pilot whales in shallower depths relative to other odontocete species and false killer whales in depths greater than 3000 m, revealing the importance of the spatial scale considered when assessing results.

The three other species sighted during this study, the smaller pantropical spotted dolphins, bottlenose dolphins and spinner dolphins, were found in mid- to shallow-depth ranges during the daytime. Based on acoustic monitoring results, these smaller species typically prefer coastal habitats that are in close proximity to the 1000 m contour, particularly during the nighttime (Howe & Lammers in prep). This likely enables efficient foraging on the productive mesopelagic boundary layer of micronekton that migrates towards shore during nighttime hours (Reid et al. 1991, Benoit-Bird & Au 2003). The results of this study show that spotted dolphins, sighted at mid-depth ranges, do not rely as heavily on shallow resting areas during the day and instead occupy deeper water coastal areas for resting. In contrast, bottlenose dolphins and spinner dolphins appear to depend on shallow habitat during the daytime, which is consistent with prior research on spinner dolphins (Norris & Dohl 1980, Norris et al. 1994, Thorne et al. 2012).

In summary, certain biases are inevitable in any citizen science project but they can be better estimated and assessed when the results are compared with those from directed scientific studies (Baird et al. 2002) and integrated into larger efforts to characterize species distributions. In addition, using a multi-approach methodology provides greater confidence in the accuracy of the overall results. For cetacean studies, further comparing results with those generated using distinct methodologies with better temporal coverage, such as passive acoustic monitoring, may further contribute to a better understanding of the overall system. Future cetacean CS projects should leverage volunteers such as fishermen and other vessel operators who possess valuable knowledge of their marine environments and understand local dolphin distribution patterns. Vessel captains and crew may also occasionally sight rare and unusual cetaceans, which is valuable information that often remains undocumented. Along with using an incidental sighting

methodology, such as the one used in this project, CS cetacean studies could also make an effort to measure the level of effort expended by volunteers in order to generate rates of observations and further expand the utility of the data. Finally, the specific tools used for data collection and communication have been shown to be a critical factor determining the success or failure of self-reporting programs (McCluskey & Lewison 2008). Therefore, CS projects should aim to utilize user-friendly technologies such as smartphone apps or SMS text messages that facilitate the transmission of data from volunteers to coordinators.

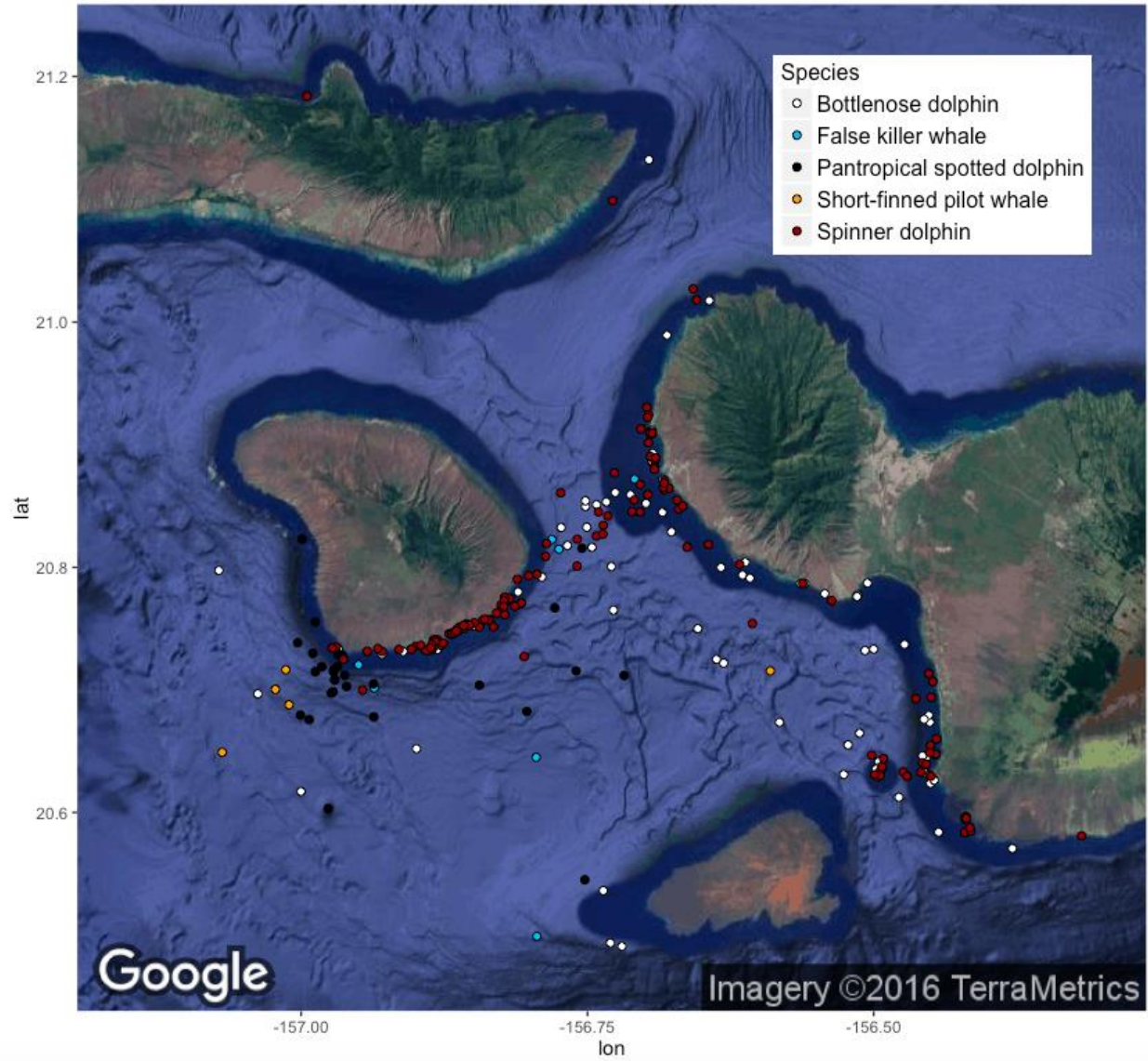
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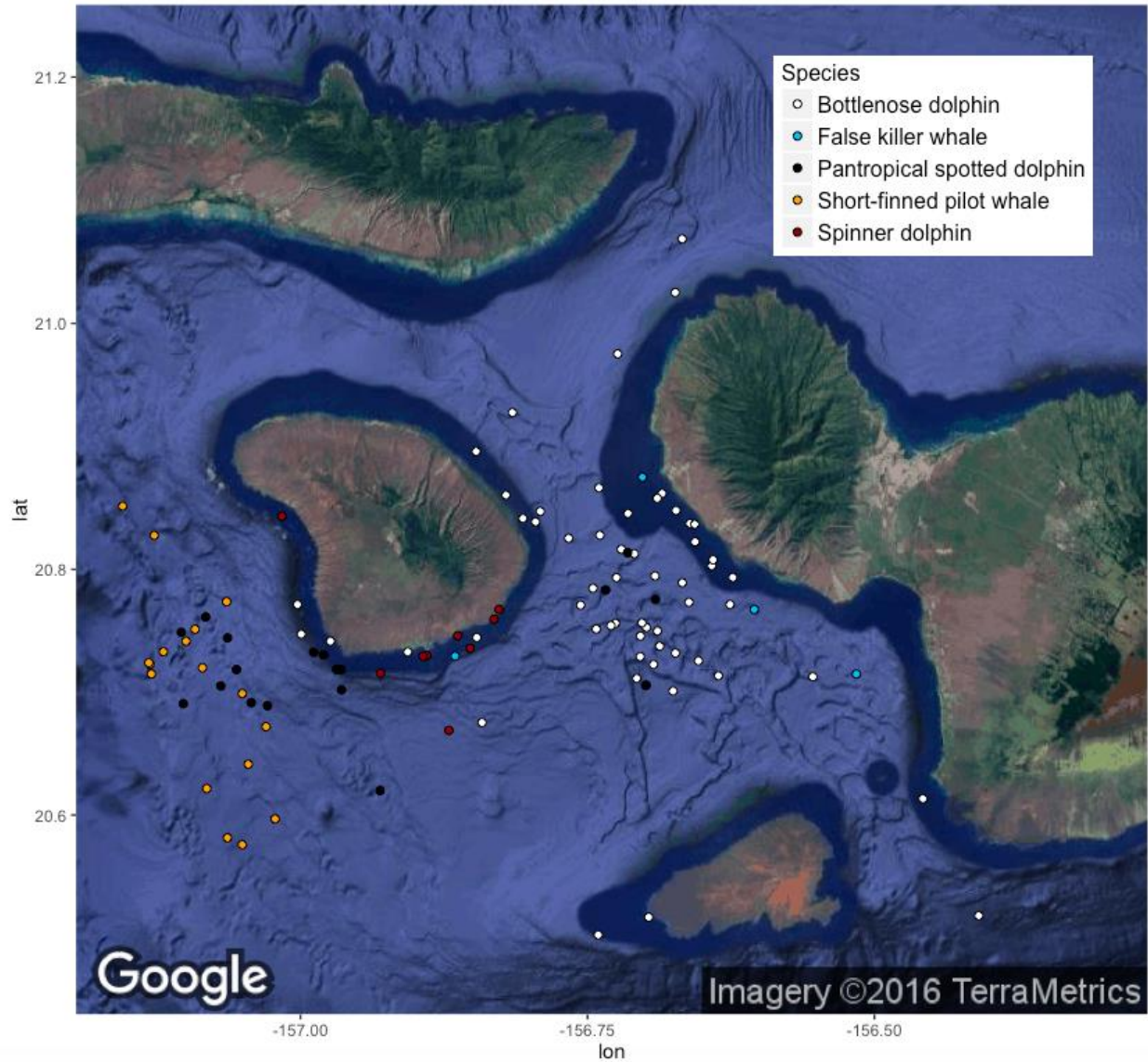
## Tables and Figures

*Table 1. Median depths of sightings (m) from directed surveys, the CS project, and combined across methods for the most common Maui Nui odontocete species. IQR values are shown in parentheses.*

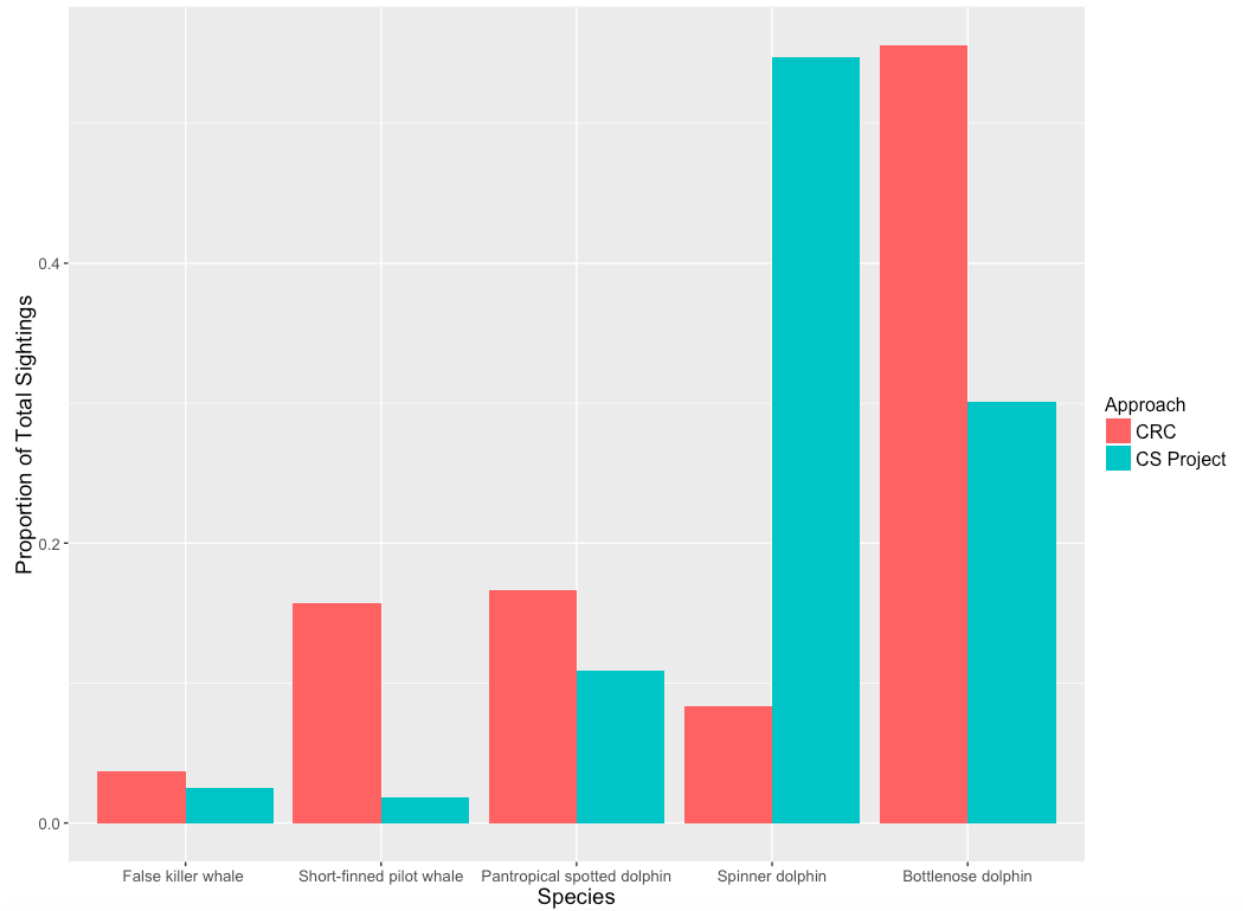
Species	Depth of Sighting (m)		
	Directed Surveys	CS project	Combined methods
Bottlenose Dolphin	86 (49.5-156.75)	67 (22.5-140)	73 (42-152)
Spinner Dolphin	156 (137-197)	68 (20-113.5)	68.5 (20-123)
False Killer Whale	82.5 (63-129)	138 (70.5-337.7)	97 (67-263.5)
Pantropical Spotted Dolphin	402.5 (206-543.75)	295.5 (147-338)	304 (161-449.75)
Short-finned Pilot Whale	686 (650-702)	434 (411-459)	666 (554-688)



*Figure 1. Map of dolphin sightings (n=276) corrected for replicate sightings from the Maui Nui community sighting project. Observations exclude species sighted only once.*

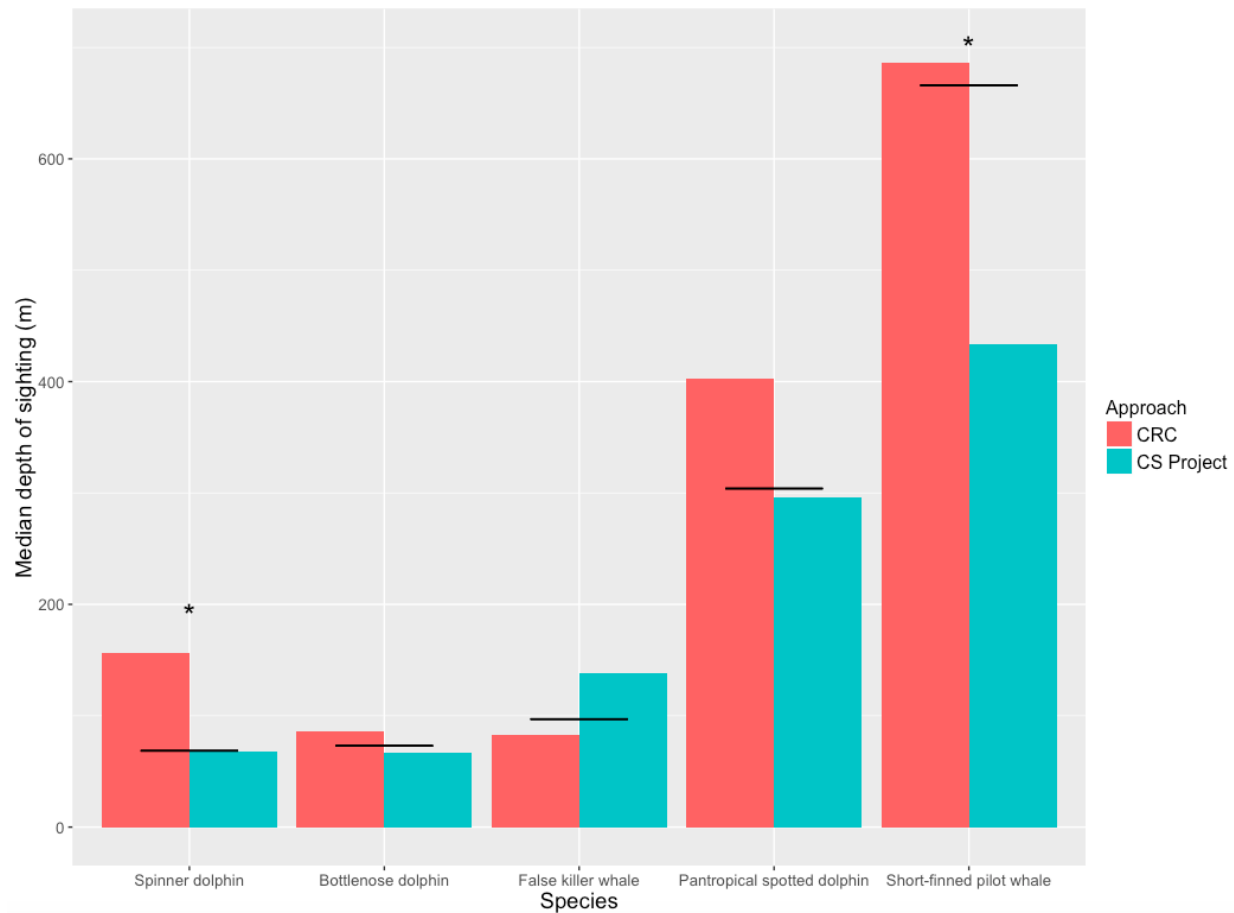


*Figure 2. Map of dolphin sightings (n=108) encountered by the Cascadia Research Collective during surveys in the Maui Nui region. Observations exclude species sighted only once.*



*Figure 3. Sighting proportions of the common odontocete species in the Maui Nui region of the total sightings collected by each survey type. The approach “CRC” designates observations made by the Cascadia Research Collective.*





*Figure 4. Comparisons of median depth of sighting (m) by approach across all commonly observed species in the Maui Nui region. Black horizontal lines indicate median depth of all sightings by species. \* indicates significant difference at  $p=0.05$  based on Wilcoxon rank sum tests. The approach “CRC” designates observations made by the Cascadia Research Collective.*

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## **CHAPTER III**

### **CONCLUSIONS**

Collecting spatiotemporal data on wild cetaceans is a challenging endeavor, as they spend their lives in a three-dimensional habitat that covers approximately 70% of the earth's surface. Much of what we know about them is based off of observational studies rather than the traditional manipulative approach of experimental design. Thus, the data gathered on cetaceans is often piecemeal, and so it becomes important to synthesize all relevant information available to help explain findings and draw the most comprehensive inferences about their ecologies. This holistic approach also helps to generate the most appropriate scientific questions to be tackled in the future. When assessed independently, the findings of these chapters provide a mere coarse understanding of Hawaiian odontocete distributions. However, relative to each other and to preexisting odontocete satellite tagging, genetic, and photo-identification data (e.g. Baird et al. 2010, Courbis et al. 2014, Mahaffy et al. 2015), these chapters help to both corroborate past studies and suggest potential prey preferences, foraging habitat, and important drivers of odontocete distributions. While this work helps inform the delineation of Biological Important Areas for Hawaiian odontocetes in relatively understudied regions (Baird et al. 2015), it has also led to many more questions regarding the distribution of species around the Hawaiian Islands in shallow waters, laying a groundwork for future odontocete research.

In this thesis, acoustic data from the first chapter showed that small dolphin species tended to use shelf areas closer to the 1000 m isobath in both Maui Nui and Oahu, especially during the nighttime. In the context of preexisting studies regarding the foraging preferences and behavior of spinner dolphins (e.g. Norris & Dohl 1980), we can be fairly confident that these patterns near the deep waters are associated with feeding due to the accessibility of the

micronekton MBCL at night. However, the prey preferences of the bottlenose dolphin, a species considered a small-bodied dolphin in this study and acoustically indistinguishable from *Stenella* spp., are relatively unknown in the Hawaiian Islands. In the Atlantic Ocean, bottlenose dolphins are known to feed on demersal and benthic fish species (Pate 2008), generally of a larger size than those of the MBCL in Hawaii. However, other evidence suggests that bottlenose dolphins do occupy the same trophic level as that of the *Stenella* species (Pauly et al. 1998), indicating that all three small odontocete species in this study may be foraging directly on the MBCL. A stable radioisotope analysis of bottlenose dolphin tissue would be useful to provide a coarse understanding of the primary prey of this species in the Hawaiian Islands.

While most research on the Hawaiian spinner dolphin has centered around Kona (e.g. Norris et al. 1994) and Oahu (Lammers 2004), this is one of the first studies to provide information on their distributions in the Maui Nui basin. With continued research on spinner dolphins in this region, predictive spinner dolphin distribution maps may soon be available around each of the MHIs. In general, our small odontocete acoustic findings in Maui Nui corroborates spinner dolphin studies around the other islands, likely reflecting that Hawaiian spinner dolphins predominately occur near deep waters at night to forage on the MBCL and return to shallow coastline habitat during the day to rest. However, the Maui Nui region is unique in its bathymetry relative to the other Hawaiian Islands, as it consists of a large shallow basin surrounded by steep sloping waters, and thus the dynamics of the MBCL in this region could be different compared to the other islands. While most of our night acoustic detections of small dolphins were made near the 1000 m isobath as expected, some night detections still occurred at shallow sites further from the deep waters. Given that spinner dolphins require large quantities of prey to meet their energetic needs and are thought to forage continuously throughout the night

(Benoit-Bird 2004), the presence of small odontocetes at nearshore shallow sites perhaps indicates that the MBCL is also present at these sites far from slope waters. It is also possible that the small odontocetes at these sites are representative of bottlenose dolphins perhaps foraging on prey sources other than the MBCL. To help resolve this question, it would be worthwhile to undertake a study using active acoustics to document the presence of the sound-scattering layer at night in the Maui Nui shelf region. It would also be interesting to better understand the outer nighttime limits of the MBCL layer around Maui Nui utilizing both passive acoustics to document odontocete occurrence at deeper isobaths and with active acoustics to directly document the SSL.

The results of the first chapter also suggest that false killer whales might be primarily driving the positive trend observed between distance to deep waters and large odontocete detections, as it is well documented that pilot whales tend to inhabit deeper slope waters (Abecassis et al. 2015). And, given that apex predator false killer whales are expected to be most influenced by foraging opportunities, these results may indicate that shallow waters benefit prey capture. To test this theory, it would be beneficial to aggregate all documented sightings of false killer whale feeding events, observed by both scientists and the public. With coordinates of the sightings, the foraging habitat could then be characterized relative to bathymetry and other oceanographic factors.

It would also be interesting to genetically identify the false killer whales that use the waters furthest from slope regions in Maui Nui to determine whether certain individuals may specialize in foraging along shallow contours. Baird et al. (2012) has documented that false killer whale population clusters differ in their depth preferences, with cluster 1 tending to prefer shallower depths, so it is likely that individuals of this cluster use the shallowest waters of the

Maui Nui basin. In addition, it would also be worthwhile to analyze satellite tagging data of all five odontocetes included in this project to assess the variation in habitat usage relative to bathymetry within species as well as across species, similar to Baird et al. (2012) analyses to determine the critical habitat of false killer whales from satellite tagging data of 27 individuals. This would help provide further insight into whether our findings in Oahu and Maui Nui are representative of the species as a whole in the Hawaiian Islands or whether the trends documented in this project are in fact unique to the study regions. Such an analysis would be fairly straightforward to complete, as satellite tagging data already exists for short-finned pilot whales (Abecassis et al. 2015) and false killer whales (Baird et al. 2010), and tagging of the more commonly-encountered spinner dolphins, pantropical spotted dolphins, and bottlenose dolphins would likely require relatively little field effort.

Based on acoustic monitoring, citizen science, and systematic surveys, these chapters demonstrate that interspecific odontocete differences exist relative to bathymetry in the Maui Nui and Oahu region of the Hawaiian Islands. Each method had drawbacks, such as the coarse taxonomic resolution of passive acoustic monitoring and the lack of nighttime coverage of both the CS project and Cascadia Research Collective's visual surveys. However, when assessed together and in the context of existing biological data, the results provide insight into various aspects of the ecology of Hawaiian odontocetes. These chapters also present viable, relatively inexpensive, and efficient alternative approaches to help understand the spatial ecology of odontocetes. While these approaches were implemented around the Hawaiian Islands, their application will likely be useful in other coastal regions as well. This may be particularly true in areas characterized by prevailing winds leading to poor visual sighting conditions or low dolphin densities where traditional vessel survey methods may not be very effective. The development

and application of innovative surveying methods should be a priority in the future to improve on the shortcomings of the methods presented here.

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